Fusarium spp. from Corn, Sorghum, and Soybean Fields in the Central and Eastern United States

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ABSTRACT

Leslie, J. F., Pearson, C. A. S., Nelson, P. E., and Toussoun, T. A. 1990. Fusarium spp. from corn, sorghum, and soybean fields in the central and eastern United States. Phytopathology 80: 343-350.

Samples of plant tissue and soil were collected from 41 corn, 18 sorghum, and 34 soybean fields in the central and southeastern United States in August 1986. Isolates of Fusarium were recovered from plant tissue, soil debris, and soil on a selective medium and identified to species. Fusarium spp. were recovered from all soils sampled. In corn, tissue usually was colonized with F. moniliforme, F. proliferatum, or F. subglutinans. F. semitectum, F. equiseti, F. oxysporum, F. graminearum, F. acuminatum, and F. chlamydosporum were recovered from debris but not from soil, and F. merismoides, F. proliferatum, and F. semitectum were recovered from soil but not from debris. In sorghum, F. moniliforme or F. proliferatum were present in 71% of the tissue samples and 18% of the debris samples. F. moniliforme was present in debris from 39% of the sorghum fields but was absent from the corresponding soil samples. F. acuminatum, F. chlamydosporum, and F. graminearum were found in debris but not in soil, and F. merismoides was found only in soil samples from sorghum fields. F. solani was present in either soil debris or soil from all sorghum fields, whereas F. oxysporum was found in debris at 44% of the sites and in soil at 72% of the sites. F. equiseti was found in both debris and soil at 33% of the sites. Fusarium spp. recovered from soybean tissue generally were different from those recovered from corn and sorghum tissue. F. oxysporum and F. solani were the predomi-

nant species and were present in 91 and 97% of the sites, respectively, whereas members of the Liseola section usually were absent. Soil and debris samples from the soybean fields contained F. acuminatum, F. equiseti, F. moniliforme, F. oxysporum, and F. solani. F. graminearum and F. semitectum were found in debris samples but not in soil samples, and F. chlamydosporum, F. compactum, F. merismoides, and F. proliferatum were found in soil samples but not in debris samples from soybean fields. F. anthophilum, F. avenaceum, and F. chlamydosporum were found in sites in southern states but not in northern states. All species found in northern states also were found in southern states, although differences in tissue, debris, and soil populations were observed. Soils of five different orders were sampled. All species were recovered from at least one Alfisol site, and all but F. avenaceum were recovered from at least one Ultisol site. F. oxysporum and F. solani were present in the soil and debris from more than 50% of the sites in each soil order, and members of Fusarium section Liseola could be found in plants at sites of each soil type. The distribution of Fusarium spp. observed in this study is consistent with the hypothesis that these fungi are widely distributed in host tissue under field conditions and that they respond to stress in the plant by taking advantage of preferential growth conditions to incite disease.

Additional keywords: stalk rot, Gibberella, Glycine max, Nectria, Sorghum bicolor, Zea mays.

The genus Fusarium is comprised of a large, complex group of fungi with ascomycete teleomorphs and contains numerous species that produce noxious secondary metabolites and/or cause serious plant diseases (51,54). Members of the genus have wide geographic and host ranges. Several species of Fusarium are associated with stalk rot (18,25), leaf spot (61), ear and kernel rot (62), and seedling blight (23,27) of corn; grain mold (11), Pokkah Boeng (22), seedling blight (22), and stalk and root rot (58,67,68) of sorghum; and Fusarium wilt (4), pod rot (63), and sudden death syndrome of soybean (19,60). Species of Fusarium have been reported to be seedborne in these three crops (12,15, 44,63,66).

Ecological studies of *Fusarium* spp. have a long history (8). General surveys of communities of *Fusarium* in other countries are fairly common, for example, communities in Australia (9), Brazil (31), Norway (1), and South Africa (47), as are those with relatively limited geographic scope (40,41,73), those from unusual climates (30), or those correlated with a particular physiological characteristic, for example, toxigenicity (2,3,43,53). In most of these surveys, samples were collected from both plant tissue and soil. Much previous work has concerned one or a few fields sam-

pled in one to several growing seasons, usually to study changes in the population structure with time (34,58,74). Many studies are limited to diseased plants of a particular species (5,10,16,27, 29,32,33,35,57,59,77).

Our goal in this study was to sample a large number of geographically diverse fields to determine if variables such as crop, climatic conditions, or soil type were correlated with the composition of populations of *Fusarium* in cultivated fields in the central and eastern United States. Most of our samples were collected from corn, sorghum, and soybean fields because these crops are grown throughout the entire region studied. Samples from this study have been analyzed previously for the presence of *Macrophomina phaseolina* (Tassi) Goid. (56).

MATERIALS AND METHODS

Sample collection. All samples were collected in August 1986. Four stalks of corn and sorghum, four roots and stems of soybean, and four cylindrical soil samples (5 cm in diameter × 13 cm long) were collected at random from fields at sites listed in Table 1. Soil samples were taken between plant rows. Where possible, tissue samples were taken from both diseased and asymptomatic plants. Plant maturity varied with geographic location.

TABLE 1. Location, soil type, climatic conditions, and crops of sampling sites

Locationa	Precipitation ^b	Temperature c	Soil typed	Cropse
Brundige, AL (Pike)	83.2 (87)	26.1 (103)	u6-1	cn
Camden, AL (Wilcox)	83.2 (87)	26.1 (103)	u6-7	cn
Clio, AL (Barbour)	83.2 (87)	26.1 (103)	e10-4 u6-7	pn sb
Greenville, AL (Butler)	83.2 (87)	26.1 (103) 26.1 (103)	u6-7	sb
Luverne, AL (Crenshaw)	83.2 (87) 83.2 (87)	26.1 (103)	u5-3	cn
Surginer, AL (Marengo)	83.2 (87)	26.1 (103)	u6-1	cn, gsg
Ггоу, AL (Pike) Brockwell, AR (Izard)	63.0 (84)	24.2 (103)	u6-6	gsg
Grays, AR (Woodruff)	59.7 (68)	26.0 (103)	a6-8	gsg, sb
Marvell, AR (Phillips)	59.7 (68)	26.0 (103)	i5-3	gsg
Patterson, AR (Woodruff)	59.7 (68)	26.0 (103)	i5-2	cn
West Helena, AR (Phillips)	59.7 (68)	26.0 (103)	i5-3	sb
Greenville, FL (Madison)	96.5 (97)	26.5 (101)	u6-1	sb
Mascotte, FL (Lake)	111.3 (98)	26.5 (100)	e10-2	gb
Starke, FL (Bradford)	96.5 (97)	26.5 (101)	u6-9	cn
Trenton, FL (Gilchrist)	96.5 (97)	26.5 (101)	e10-1	cn, sb
Blitchton, GA (Bulloch)	79.2 (85)	27.0 (105)	u1-3	sb
Boston, GA (Thomas)	65.8 (69)	26.8 (104)	u6-1	cn
Broadhurst, GA (Wayne)	79.2 (85)	27.0 (105)	u1-3	cn
Guyton, GA (Effingham)	79.2 (85)	27.0 (105)	u1-3	en et geg nn el
Morgan, GA (Calhoun)	65.8 (69)	26.8 (104)	u6-1	cn, ct, gsg, pn, sl
Pavo, GA (Thomas)	65.8 (69)	26.8 (104)	u6-1 u1-3	cn
Pembroke, GA (Liberty)	79.2 (85)	27.0 (105) 26.8 (104)	u6-1	sb
Sutton's Corner, GA (Clay)	65.8 (69) 56.9 (82)	22.7 (102)	a1-3	cn, fsg, sb
Greenup, IL (Cumberland)	47.8 (73)	22.7 (101)	a6-7	cn, gr, sb
Marine, IL (Madison)	56.9 (82)	22.7 (101)	a1-3	cn, gr
St. Elmo, IL (Fayette)	69.6 (97)	21.1 (101)	a7-4	cn, gr, sb
Belleville, IN (Hendricks) Knightstown, IN (Henry)	69.6 (97)	21.1 (101)	a7-4	cn, sb
Terre Haute, IN (Vigo)	61.5 (86)	21.4 (101)	m2-4	fr, sb, gsg
Booneville, MO (Cooper)	62.6 (94)	23.6 (106)	m2-4	cn, gr, sb
Coal, MO (Henry)	62.6 (94)	23.6 (106)	u6-4	cn
Odessa, MO (Lafayette)	61.3 (95)	22.5 (96)	m2-4	cn, sb, gsg
Tightwad, MO (Henry)	62.6 (94)	23.6 (106)	u6-4	gsg, sb
Williamsburg, MO (Callaway)	51.1 (79)	23.0 (106)	a1-2	gr, sb, gsg
Wright City, MO (Warren)	51.1 (79)	23.0 (106)	a7-6	cn, gr, sb
Charleston, MS (Tallahatchie)	61.2 (65)	26.4 (103)	a2-2	cn
Crowder, MS (Quitman)	61.2 (65)	26.4 (103)	a2-2	cn, gsg, sb
Holcomb, MS (Grenada)	63.8 (64)	25.5 (102)	a2-2	ct, gsg, sb
Kusciusko, MS (Attala)	63.8 (64)	25.5 (102)	u6-3	cn, cp, sb
Lambert, MS (Quitman)	61.2 (65)	26.4 (103)	a2-2	ri
Stallo, MS (Neshoba)	62.7 (63)	25.7 (103)	u6-3	cn cn gcg
Viaden, MS (Carrol)	63.8 (64)	25.5 (102)	a7-9 u6-5	cn, gsg cn, sb
Buie, NC (Robeson)	77.0 (83)	25.1 (104) 23.5 (103)	u5-3	sb
Climax, NC (Guilford)	61.0 (78)	24.3 (104)	u5-3	sb
Gray's Chapel, NC (Randolph)	54.6 (66) 54.6 (66)	24.3 (104)	u5-3	gsg
Maple Springs, NC (Randolph)	61.0 (78)	23.5 (103)	u5-3	cn, gsg
Pleasant Garden, NC (Guilford) Raeford, NC (Hoke)	77.0 (83)	25.1 (104)	u6-10	cn, sb
Ramseur, NC (Randolph)	54.6 (66)	24.3 (104)	u5-3	cn, tb
Red Springs, NC (Robeson)	77.0 (83)	25.1 (104)	u6-5	cn
Bachman, OH (Preble)	60.5 (83)	21.6 (100)	a7-4	cn, gr, sb
Canaanville, OH (Athens)	55.9 (78)	20.5 (102)	i8-4	cn
Carrol, OH (Fairfield)	54.9 (92)	20.9 (101)	a7-4	cn, sb
Frost, OH (Athens)	55.9 (78)	20.5 (102)	i8-4	sb
Guysville, OH (Athens)	55.9 (78)	20.5 (102)	i8-4	cn
Steward, OH (Athens)	55.9 (78)	20.5 (102)	i8-4	fsg
Centenary, SC (Marion)	67.8 (76)	26.0 (105)	u6-5	cn, sb
Estil, SC (Hampton)	76.5 (82)	26.4 (105)	u1-3	gsg
Fork, SC (Marion)	67.8 (76)	26.0 (105)	u6-5	cn, sb, tb
Hampton, SC (Hampton)	76.5 (82)	26.4 (104)	u1-2	cn, fr
Luray, SC (Hampton)	76.5 (82)	26.4 (104)	u1-3	cn, sb
Walterboro, SC (Colleton)	76.5 (82)	26.4 (104)	u1-2	cn, sb
Fairplain, WV (Jackson)	62.5 (80)	22.1 (102)	i8-4 i8-6	gr
Powell, WV (Kanawha)	61.0 (78)	23.5 (103)	10-0	gr

a City, state (county).

^b Rainfall in centimeters from January through August 1986 (percent average rainfall).

^c Average temperature in ^oC from May through August 1986 (percent average temperature).

d Based on the classification of Soil Survey Staff, Soil Conservation Service, U.S. Department of Agriculture (64). All classifications are given to the level of great group. Descriptions from Brady (7). "a" soils are Alfisols which are medium to high in bases, have a gray to brown surface horizon, and have subsurface horizons of clay accumulation. "e" soils are Entisols and have no pedogenic horizons. In our samples, these soils usually had textures of loamy fine sand and were high in minerals resistant to weathering. "i" soils are Inceptisols that have weakly differentiated horizons; materials in the soils have been altered or removed and have not been accumulated. "m" soils are Mollisols that had nearly black friable organic-rich surface horizons high in bases. "u" soils are Ultisols that are low in bases and have subsurface horizons of clay accumulation.

cn = corn, ct = cotton, fsg = forage sorghum, fr = forest, gb = green beans, gr = grass, gsg = grain sorghum, pn = peanut, ri = rice, sb = soybeans, tb = tobacco.

Tissue preparation. Stalks of corn and sorghum were stripped of leaves and placed in paper bags in the field. Roots of soybean were removed, shaken free of soil, and placed in paper bags in the field. Tissue samples were rinsed with running tap water in the laboratory to remove soil and most of the nodules from the soybean roots. Root samples of soybean were surface disinfested in 0.8% NaOCl for 1 min and then blotted dry with paper toweling. All tissue samples were dried in a forced-air oven for 24 hr at 28 C. Dried samples were ground in a Wiley mill through a 20-mesh (850-µm) screen. Ground material was stored in capped test tubes at 4 C and cultured within 2 mo. Dried material was used for all tissue analyses.

Soil preparation. Soil was air dried for 24 hr at 28 C and then sieved through a 20-mesh screen. Material retained on the screen was termed "debris," and material that passed through the screen was termed "soil." Dried soil was stored in capped test tubes at 4 C and cultured within 2 mo. Isolates of *Fusarium* recovered from soil and debris were analyzed separately.

Isolation and identification of Fusarium spp. Fusarium spp. were isolated from soil, debris, and plant tissue. Small quantities of soil (10-30 mg) were sprinkled on the surface of a selective medium (52) as modified by Nelson et al (54) in petri dishes. Pieces of ground plant tissue and pieces of debris screened from the soil samples were placed on the selective medium in petri dishes and incubated for 7 days under fluorescent lights on a

TABLE 2. Distribution of *Fusarium* spp. within host tissue, soil, and debris from corn fields

Location	Tissue	Debris	Soil
Brundige, AL	eq,ª mo, se	ox	eq, ox, so
Camden, AL	mo	ch, ox	ox, so
Surginer, AL	eq, mo	ox, so	ox, so
Troy, AL	mo, se	ox	me, ox
Patterson, AR	mo	No sample	eq, ox
Starke, FL	mo	ox	ox
Trenton, FL	mo	so	ox
Boston, GA	mo, se	No sample	ac, ox
Broadhurst, GA	mo	eq, ox, so	so
Guyton, GA	ch, mo, se	eq, ox, so	ox, so
Morgan, GA	eq, mo, se	ox, so	ox, so
Pavo, GA	ch, eq, mo, ox	mo, ox, so	eq, pr, so
Pembroke, GA	mo, ox, se	ac, eq, ox	ox, se
Greenup, IL	gr, mo, se, su	ac, eq, ox, so	co, eq, ox, so
Marine, IL	ac, mo, pr	so	me
St. Elmo, IL	mo, su	ac, eq, ox, so	ac, eq, ox, se
Belleville, IN	ac, gr, mo, pr	ac, eq, so	eq, so
Knightstown, IN	ac, mo	ox, so	eq, so
Booneville, MO	eq, mo, ox	so	so
Coal, MO	mo	so	ox
Odessa, MO	mo, pr	eq, so	so
Wright City, MO	gr, mo, pr	so	ox, so
Charleston, MS	mo	eq, ox, so	ox, so
Crowder, MS	mo, se	ac, mo, ox, so	ox
Kusciusko, MS	mo	No sample	ox, so
Stallo, MS	eq, mo, se	ox, so	eq, ox
Viaden, MS	mo	eq, mo, ox	ox, so
Buie, NC	mo, ox	co, ox	eq, ox, so
Pleasant Garden, NC	eq, mo	ac, eq, pr	ox, so
Raeford, NC	mo, se	so	ox, so
Ramseur, NC	mo, ox	ox, so	ox
Red Springs, NC	mo, se, su	co, so	so
Bachman, OH	mo, su	eq, ox, so	eq, ox, so
Caananville, OH	gr, mo, pr	so	eq, ox, so
Carrol, OH	gr, mo, pr	ac, mo, so	so, su
Guysville, OH	pr, se	eq, ox, so	so
Centenary, SC	mo	eq, ox, so	ox, so
Fork, SC	mo	ox, so	me, ox
Hampton, SC	eq, mo, se	so	ox, so
Luray, SC	mo	mo, ox, pr	ox, so
Walterboro, SC	ac, mo, ox, se	ox, so	so

^a ac = F. acuminatum, ch = F. chlamydosporum, co = F. compactum, eq = F. equiseti, gr = F. graminearum, me = F. merismoides, mo = F. moniliforme, ox = F. oxysporum, pr = F. proliferatum, se = F. semitectum, so = F. solani, su = F. subglutinans.

12-hr day/night schedule at 22-24 C. After 7 days, colonies of Fusarium that differed in morphological characters were subcultured on carnation leaf agar (CLA) (20) and potato-dextrose agar (PDA) slants (54), incubated as described above for 10-14 days, and identified to species according to Nelson et al (54). Selected soil and tissue samples are available from J. F. Leslie and cultures are available from P. E. Nelson for further study.

RESULTS

Species of *Fusarium* recovered in this study are listed in Tables 2-6. Tables 2-5 list individual sites by crop and include specific data on the species recovered from soil, debris, and tissue at each location. Table 6 is a summary of these data expressed as relative frequencies. All soils contained *Fusarium* spp., but the composition of populations in soil, debris, and plant tissue differed substantially. Differences related to crop were much greater than differences attributable to geographic distribution.

Host distribution. Most of our samples were from corn. sorghum, and soybeans. Tissue from corn plants was colonized universally with one of the members of the Liseola section: F. moniliforme Sheldon, F. proliferatum (Matsushima) Nirenberg, or F. subglutinans (Wollenw. & Reinking) Nelson, Toussoun, and Marasas (Tables 2 and 6). None of the stalks was free of Fusarium. Species distribution within the tissue differed from that observed within the soil and debris samples. F. oxysporum Schlecht. emend. Snyd. & Hans. and F. solani (Mart.) Appel & Wollenw. emend. Snyd. & Hans. were present at 66-76% of the sites in both debris and soil. Species distributions in debris and soil from corn fields were similar with the exceptions of F. moniliforme and F. chlamydosporum Wollenw. & Reinking. which were recovered from debris but not from soil, and F. merismoides Corda, F. semitectum Berk. & Rav., and F. subglutinans, which were recovered from soil but not from debris.

Distribution of Fusarium spp. in sorghum tissue (Tables 3 and 6) was similar to that found in corn with the exceptions of the relatively rare F. acuminatum Ell. & Ev. sensu Gordon, F. avenaceum (Fr.) Sacc., F. solani, and F. subglutinans. F. moniliforme and/or F. proliferatum were present in 89% of the sorghum tissue samples. No Fusarium spp. were recovered from a small secondary tiller collected in Terre Haute, IN. Species distributions from both the soil and the debris samples differed sharply from that observed in the tissue samples. F. solani was present in either the soil or the debris of all of the sorghum

TABLE 3. Distribution of Fusarium spp. within host tissue, soil, and debris from sorghum fields

Location	Tissue	Debris	Soil		
Troy, AL ^a	mo,b pr	mo, ox, so	ox, so		
Brockwell, AR ^a	mo, pr	ox, so	ox, so		
Grays, AR ^a	mo, ox	mo, pr, so	ox, so		
Marvell, ARa	mo	ac, mo, ox	ox, so		
Morgan, GA ^a	mo	ch, so	so		
Greenup, IL ^c	eq, pr, se	so	ox		
Terre Haute, IN ^a	No Fusarium	eq, mo, so	eq, ox, so		
Terre Haute, INa	mo, pr	so	ox		
Odessa, MO ^a	eq, gr, mo, pr	ac, eq, ox, so	ox, so		
Tightwad, MO ^a	mo	mo, pr, so	eq, so		
Williamsburg, MO°	mo, pr	eq, so	eq, so		
Crowder, MS ^a	av, ch, eq, se	No sample	eq, so		
Holcomb, MS ^a	eq, mo, pr, se	eq, ox, so	ox, so		
Viaden, MS ^a	mo, se	ox, so	me, so		
Maple Springs, NCa	eq	mo	ox, so		
Pleasant Garden, NCa	ch, eq, mo, so	mo, ox, so	ox, so		
Steward, OH ^c	mo, se	eq, ox, so	eq, ox		
Estill, SC ^a	ch, mo, se	eq, gr, so	ox, so		

^a Grain sorghum.

bac = F. acuminatum, av = F. avenaceum, ch = F. chlamydosporum, eq = F. equiseti, gr = F. graminearum, me = F. merismoides, mo = F. moniliforme, ox = F. oxysporum, pr = F. proliferatum, se = F. semitectum, so = F. solani.

c Forage sorghum.

fields, and F. oxysporum was present in the soil or the debris from 78% of the fields. Species distributions in debris and soil from sorghum fields differed in that F. moniliforme was present in debris at 41% of the sites but was not detected in the soil from any of the sites. F. acuminatum, F. chlamydosporum, and

TABLE 4. Distribution of Fusarium spp. within host tissue, soil, and debris from soybean fields

Location	Tissue	Debris	Soil		
Greenville, AL	co,a eq, ox, pr, so	so	eq, ox, so		
Luverne, AL	ox	ox, so	me, ox, so		
Grays, AR	so	No sample	so		
West Helena, AR	eq, ox, so	eq	co, ox, so		
Greenville, FL	ox	ox, so	co, ox, so		
Trenton, FL	No sample	so	ox, so		
Blitchton, GA	eq, ox, so	ox, so	ox, so		
Morgan, GA	ox, se, so	ox, so	co, eq, mo, ox, so		
Sutton's Corner, GA	eq, ox, so	ox, so	ox, so		
Greenup, IL	so	so	ox		
Marine, IL	ox, so	ac, eq	me, ox		
Marine, IL	eq, ox, so	ox, so	ox, so		
Belleville, IN	eq, ox, so	ox, so	ox, pr		
Knightstown, IN	eq, ox, so	eq, so	eq, so		
Terre Haute, IN	ox, so	gr, ox, so	ox		
Booneville, MO	so	so	so		
Odessa, MO	ox, so	ox, so	eq, ox, so		
Tightwad, MO	eq, ox, so	so	ox, so		
Williamsburg, MO	so	so	so		
Wright City, MO	ox, so	so	ac		
Crowder, MS	so	ac, so	ac, ox		
Holcomb, MS	eq, ox, so	eq, ox, so	ox		
Kusciusko, MS	so	ox, so	ch, so		
Buie, NC	so	ox, se	ox		
Climax, NC	so	ox, so	ox, so		
Gray's Chapel, NC	eq, ox, so	mo, ox, so	ox		
Raeford, NC	so	eq, ox, so	ox		
Bachman, OH	eq, ox, so	eq, ox, so	eq, ox, so		
Carrol, OH	ox	eq, ox, so	ox, so		
Frost, OH	so	ac, ox, so	ox, so		
Centenary, SC	ox	ox, so	ox, so		
Fork, SC	ox	eq, ox	eq, ox		
Luray, SC	co, eq, ox, se, so	ox, so	ox, so		
Walterboro, SC	ox, so	ox	eq, ox		

^a ac = F. acuminatum, ch = F. chlamydosporum, co = F. compactum, eq = F. equiseti, gr = F. graminearum, me = F. merismoides, mo = F. moniliforme, ox = F. oxysporum, pr = F. proliferatum, se = F. semitectum, so = F. solani, su = F. subglutinans.

F. graminearum Schwabe were found in debris but not soil, and F. merismoides was found in soil but not in either tissue or debris.

The distribution of Fusarium spp. in soybean tissue (Tables 4 and 6) was different from that in either corn or sorghum tissue. Species distribution in soybean field soil and debris did not differ greatly from that found in corn and sorghum field soil and debris. In soybean tissue, the species distribution resembled that found in soybean field soil and debris. All of the species in the tissue were found in either the soil or the debris; no tissue sample was free of Fusarium. F. oxysporum and F. solani predominated and were present at 91 and 97% of the sites, respectively. Species distributions in debris and soil from soybean fields were similar with the exceptions of F. graminearum and F. semitectum, which were found in debris but not in soil, and F. chlamydosporum, F. compactum (Wollenw.) Gordon, F. merismoides, and F. proliferatum, which were found in soil but not debris.

Geographic distribution. To examine geographic distribution trends, we divided the isolates into two groups: "North" and "South" (Table 7). F. anthophilum (A. Braun) Wollenw., F. avenaceum, and F. chlamydosporum were found at sites in the southern states but not in the northern states; all species found in northern states also were found in southern states. F. moniliforme was present in soils from sites in the southern but not the northern states. In tissue samples, F. compactum was found in the South but not the North, whereas F. graminearum was found in the North but not the South. F. semitectum and F. moniliforme were more frequent in plant tissue from the South than from the North. In debris samples, F. compactum was found in the South but not in the North, whereas F. subglutinans was found in the North but not the South. Three species, F. acuminatum, F. equiseti (Corda) Sacc., and F. solani, were at more northern than southern sites, whereas F. oxysporum was more common in the South than in the North. In soil samples, F. graminearum and F. subglutinans were found at sites in the North but not in the South. F. equiseti was more common at sites in the North than in the South, whereas F. oxysporum was more common at sites in the South than in the North.

Soil-type distribution. To examine the general influence of soil type, we divided the isolates into five groups (Table 1) based on the order of the soil group (7). Most of our samples were from sites with either Alfisol or Ultisol soils, and all species except *F. anthophilum* and *F. avenaceum* were recovered from at least one Alfisol and at least one Ultisol site (Table 8). *F. oxysporum* and *F. solani* were present in the soil or debris from more than 50% of the sites in each of the five different soil orders. *F. moniliforme* and *F. solani* were found in plants at sites of each soil

TABLE 5. Distribution of Fusarium spp. within host tissue, soil, and debris from fields planted to various hosts

Location	Host	Tissue	Debris	Soil
Clio, AL	Peanut	mo, a se, so	so	pr
Mascotte, FL	Green beans	No sample	so	co, ox
Morgan, GA	Cotton	No sample	ox, so	ox, so
Morgan, GA	Peanut	eq, ox, so	ox, so	eq, ox, so
Morgan, GA	Peanut	ox, pr, so	ox, so	co, ox, so
Marine, IL	Grass	No sample	ac, ox, se, so	ox, so
St. Elmo, IL	Grass	No sample	ac, mo, so	so
Belleville, IN	Grass	No sample	so	gr, ox, so
Terre Haute, IN	Forest	No sample	ox, so	ox, so
Booneville, MO	Grass	No sample	so	se, so
Williamsburg, MO	Grass	No sample	mo, pr, so	eq, so
Wright City, MO	Grass	No sample	ox	ox, so
Holcomb, MS	Cotton	ox	ch, mo, ox, pr, so	ch, so
Kusciusko, MS	Cowpea	ox, so	No sample	ox, so
Lambert, MS	Rice	No sample	eq, se	ch, eq, ox, so
Ramseur, NC	Tobacco	No sample	ox	ox, so
Bachman, OH	Grass	No sample	eq, mo, so	pr, so
Fork, SC	Tobacco	mo, ox, pr, se	so	ox, so
Hampton, SC	Forest	No sample	ox	an
Fairplain, WV	Grass	No sample	ac, eq, so	so
Powell, WV	Grass	No sample	ox, so	gr, so

 $^{^{}a}$ ac = F. acuminatum, an = F. anthophilum, ch = F. chlamydosporum, co = F. compactum, eq = F. equiseti, gr = F. graminearum, me = F. merismoides, mo = F. moniliforme, ox = F. oxysporum, pr = F. proliferatum, se = F. semitectum, so = F. solani, su = F. subglutinans.

TABLE 6. Differential distribution of Fusarium spp. in tissue (T), debris (D), and soil (S) according to crop field

	Corn				Sorghum			Soybean	255 745	Total*		
Species	T	D	S	T	D	S	T	D	S	T	D	S
F. acuminatum	10 ^b	18	5		12			9	6	4	14	4
F. anthophilum												1
F. avenaceum				6					****	1		
F. chlamydosporum	5	3		17	6				3	5	3	3
F. compactum		5	3				6		9	2	2	5
F. equiseti	20	34	27	33	35	22	36	24	21	28	28	22
F. graminearum	12			6	6			3		6	2	2
F. merismoides			7			6			6			5
F. moniliforme	98	13		78	41			3	3	57	16	1
F. oxysporum	15	66	73	6	47	67	70	67	82	36	60	72
F. proliferatum	17	5	2	39	12		3		3	17	6	4
F. semitectum	34		5	33			6	3		24	3	1
F. solani		76	68	6	88	78	85	85	65	34	81	72
F. subglutinans	10		2							4		1
Total number of sites	41	38	41	18	17	18	33	33	34	98	108	114

^a Total includes data from all sites, not just corn, sorghum, and soybean.

TABLE 7. Geographical distribution of *Fusarium* spp. in tissue (T), debris (D), and soil (S)

		North ^a	South ^b				
Species	T	D	S	T	D	S	
F. acuminatum	3°	23	5	1	6	3	
F. anthophilum						1	
F. avenaceum				1			
F. chlamydosporum				5	5	4	
F. compactum			2	2	3	6	
F. equiseti	8	36	32	17	22	17	
F. graminearum	5	2	2		2		
F. merismoides			5			6	
F. moniliforme	14	14		40	17	1	
F. oxysporum	11	41	55	19	73	83	
F. proliferatum	11	5	5	4	6	1	
F. semitectum	4	2	2	18	3	1	
F. solani	13	95	75	19	72	73	
F. subglutinans	3	19 4.34 .34	2	1			
Total numbers of sites	34	44	44	64	64	70	

^a North = Illinois, Indiana, Missouri, Ohio, and West Virginia.

type. Differences in distribution patterns of the other species generally were difficult to discern because of the relatively small sample sizes.

Meteorological influences. Precipitation from January through August was used to determine the amount of moisture available to the crop during the growing season. At most locations, the months of January through July were much dryer than normal and the month of August was much wetter than normal. Similarly, for most sites, the average temperature during May, June, and July was above normal, and it was average or slightly below average during August. Because our samples were taken in early to mid-August, values given in Table 1 may not reflect the full extent of the temperature and moisture stress to which the plants were subjected before sampling.

DISCUSSION

In corn and sorghum tissue, F. moniliforme was the predominant species. This fungus can be seedborne internally in symptomless, apparently healthy corn kernels (21,50,66). When combined, these findings have potentially serious implications because some strains of this fungus can produce potent mycotoxins associated with serious animal and human diseases (24,36,46, 49,72) and because this fungus is commonly associated with basic

human dietary staples such as corn (46). In addition to humans, the following animals also are affected: baboons, chicks, donkeys, ducklings, horses, mice, rats, and sheep. Until recently, the chemical nature of the mycotoxins in *F. moniliforme* has been, for the most part, unknown. Recently, a group of toxigenic compounds, the fumonisins, produced by this fungus have been characterized chemically (6). These compounds have been shown to have cancer-promoting activity (24) and to cause equine leukoencephalomalacia (48). The widespread occurrence of this fungus indicates that the potential exists for toxicological problems in corn and sorghum in the United States. Further testing will be required, however, to determine what portion of the population of this species produces these compounds and the environmental conditions that favor toxin production.

F. merismoides was isolated from soil at several of the locations sampled during this survey. Although this fungus was present in low numbers only, it was distributed widely, and the distribution pattern did not seem to be influenced by environmental conditions. In some cases, environmental conditions may influence the number of cultures of F. merismoides obtained (30), but they do not seem to be the controlling factor. We also have obtained cultures of F. merismoides from 13 geographic locations within the United States, ranging from Florida to North Dakota, and from Australia, Austria, China, England, Germany, Honduras, Philippines, South Africa, Taiwan, Thailand, and Zimbabwe (P. E. Nelson, unpublished). Thus, this fungus is widely distributed even though it usually is recovered only in small numbers.

F. chlamydosporum has a higher optimum temperature for growth than most other species of Fusarium, and it occurs as a saprophyte in soil and on other substrates in tropical and subtropical areas (47). This species also is commonly associated with seed of bean, millet, peanut, and sorghum in warmer areas of the world (50) and previously has been recovered from slash pine and soil in Florida, soil in Mississippi, corn in South Carolina, and oats and sorghum in North Carolina (P. E. Nelson, unpublished). In this survey, F. chlamydosporum was recovered in low numbers from sorghum tissue from Mississippi, South Carolina, and North Carolina, and from sorghum soil debris from Georgia. In addition, cultures were obtained from cotton soil and debris and rice soil from Mississippi (Table 5). Data from this survey are consistent with the previously known distribution of this species.

F. sambucinum Fuckel was not recovered from any of the plant tissue, soil debris, or soil samples cultured in this study. This absence may reflect the environmental conditions at the time samples were collected or may indicate that the climate in the sampling areas was not favorable for growth of this species. Burgess et al (9) found that F. sambucinum was restricted to cold temperate and alpine areas of eastern Australia. In the United

^b Percentage of sites at which species was identified.

^b South = Alabama, Arkansas, Florida, Georgia, Mississippi, North Carolina, and South Carolina.

^c Percentage of sites at which species was identified.

TABLE 8. Soil-type distribution of Fusarium spp. in tissue (T), debris (D), and soil (S)

		Aª			Е			I			M			U	
Species	T	D	S	T	D	S	T	D	S	Т	D	S	T	D	S
F. acuminatum	10 ^b	26	10					38			10		2	4	2
F. anthophilum															2
F. avenaceum	3														
F. chlamydosporum	3	3	5										8	4	2
F. compactum			3		***	25			11				4	4	6
F. equiseti	27	43	30				14	50	33	25	30	20	31	16	19
F. graminearum	13		3				14		11	13	10			2	
F. merismoides			8												6
F. moniliforme	50	23		100			57	13		50	10		63	16	2
F. oxysporum	33	49	59			75	14	63	67	38	40	60	39	75	85
F. proliferatum	23	9	5			25	29			38			12	6	2
F. semitectum	20	6	3	50			29					10	31	2	2
F. solani	37	91	73	50	100	25	29	75	78	38	100	80	27	73	74
F. subglutinans	10		3									• • •	2	•••	• • •
Total number of sites	30	35	37	2	4	4	7	8	9	8	10	10	51	51	54

^a Soil type: A = Alfisols, E = Entisols, I = Inceptisols, M = Mollisols, U = Ultisols.

States, this species has been recovered from soil and soil debris from rangeland and subalpine soils in Helena and Butte, MT, and Mount Crested Butte, CO, from debris from a pasture in Michigan, and from tundra at the Arctic Research Center at Coldfoot, AK (P. E. Nelson, *unpublished*). Even though some of the areas in the midwestern United States sampled in this survey are cold temperate areas, environmental conditions at these sites do not compare with alpine sites in eastern Australia and sites in Alaska where this fungus was recovered in large numbers.

Fusarium spp. are associated with both symptomatic and asymptomatic crop plants. Data from this survey are consistent with previous observations that colonization is systemic even in asymptomatic plants and that the fungal flora within the plant is different, at least in frequency, from that found in either field soil or debris (21,37). This association makes it difficult to discern if the fungus is the primary disease causal agent, a secondary invader, or an endophyte. For example, several species of Fusarium have a long-term association with stalk rot of corn (5,10,16, 17,25-27,29,32,33,35,57,59,69-71,75). This association may bias our thinking about these fungi and prevent us from discerning a problem, such as a mycotoxicosis, or could lead to the misdiagnosis of the true causal agent of the disease. Similarly, the belief that all isolates of any particular species of Fusarium are equally pathogenic needs to be viewed with great caution because many of our tissue samples were taken from apparently "healthy" plants. From the data in this survey, it is apparent that a study of a population of a species of Fusarium is incomplete unless both healthy and diseased plants are studied. The possibility of different populations that vary in virulence remains open.

The composition of the fungal population is likely to vary with time of year and the environmental conditions associated with a particular field or growing season (74,77). Thus, our survey presents a snapshot of the population taken over a broad geographic area rather than a continuous picture that could be made by following the populations at fewer locations through an entire growing season. The snapshot raises some interesting questions. For example, the relative scarcity of F. moniliforme in corn soil and debris as compared with tissue suggests that the pathogen could be seedborne and that most of the inoculum in a field is introduced on seed planted at the beginning of each growing season. Alternatively, F. moniliforme could be limited to plant tissue where it thrives during the growing season and survives in dormancy, perhaps as thickened hyphae, the rest of the year (45). Experiments to determine whether fungal strains present on (or in) the seed are preferentially present in the mature plant and to determine the relative importance of seedborne and soilborne strains in the infection of the host will be needed to resolve this issue.

The fungi retained from this survey should form a good working collection for the study of variability and population genetics

in various species of Fusarium. The widespread distribution of species in the Fusarium section Liseola offers the opportunity for relatively easy collection of large numbers of geographically diverse isolates. By using selectively neutral markers such as isozymes, vegetative compatibility groups (14), or DNA restriction fragment length polymorphisms (28), it should be possible to determine if the isolates we have collected are part of a large panmictic population or if there are a number of distinct local populations.

Many species of Fusarium are viewed as opportunistic or weak pathogens that are capable of attacking only plants that were weakened previously by some other stress. Certainly, stresses such as those induced by drought, hail, and insects are known to affect the amount of stalk rot caused by F. moniliforme in corn (13,42,55), and disease incidence can be lowered if preventative measures, such as following a proper irrigation schedule (65), are employed. These fungi seem to be well adapted to such a life style. For example, F. moniliforme is known to grow at quite low water potential (76), and F. graminearum is known to efficiently catabolize stress-related nitrogen sources (38,39). Such metabolic traits are consistent with the hypothesis that these fungi are widely distributed in host tissue under field conditions and react to stress in the plant by taking advantage of preferential growth conditions to incite disease.

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^b Percentage of sites at which species was identified.

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