Pathogenicity of Three Species of *Pythium* to Seedlings and Mature Plants of Grain Sorghum

R. G. Pratt and G. D. Janke

Assistant professor and research associate, respectively, Texas Agricultural Experiment Station, Texas A&M University Agricultural Research and Extension Center, P.O. Box 10607, Corpus Christi 78410. Present address of senior author: Agricultural Research, Science and Education Administration, U.S. Department of Agriculture, and Department of Plant Pathology and Weed Science, Mississippi State University, P.O. Drawer PG, Mississippi State 39762.

The authors are grateful to R. A. Frederiksen, Department of Plant Sciences, Texas A&M University, and D. T. Rosenow, Texas Agricultural Experiment Station, Lubbock, for assistance in locating diseased plants in the field; to J. W. Johnson, Texas Agricultural Experiment Station, Lubbock, for supplying seed of greenbug-susceptible and -resistant sorghum hybrids; and to F. R. Miller, Department of Agronomy, Texas A&M University, for nursery space and care of plants.

Accepted for publication 5 February 1980.

ABSTRACT

PRATT, R. G., and G. D. JANKE. 1980. Pathogenicity of three species of *Pythium* to seedlings and mature plants of grain sorghum. Phytopathology 70:766-771.

Pythium graminicola, P. myriotylum, and *P. periplocum* were isolated from mature plants of grain sorghum in Texas with symptoms of root rot and lodging. Morphological characteristics of *P. graminicola* isolates are described and taxonomic concepts are evaluated. Pathogenicity of the three *Pythium* spp. to sorghum was evaluated by inoculating inbred plants at five stages of growth. *P. graminicola* and *P. myriotylum* caused pre- and postemergence damping-off whereas *P. periplocum* caused no damping-off. *P. graminicola* greatly reduced sizes of root systems of plants inoculated at 2, 4, and 8 wk of age, whereas *P. myriotylum* and *P. periplocum* caused little or no damage. *P. graminicola* caused severe necrosis of roots of mature plants whereas *P. myriotylum* and *P. periplocum* caused little necrosis. Four sorghum hybrids differed in susceptibility to *P. graminicola* at maturity, but not at 2 wk of age. Susceptibility was not correlated with resistance to greenbug (*Schizaphis graminum*). Stalk rot occurred in some plants of all hybrids inoculated in the stalks with *P. graminicola.*

Species of *Pythium* Pringsheim are often associated with root diseases of sorghum (*Sorghum bicolor* [L.] Moench.) or are known to be pathogenic to seedlings. However, despite numerous reports, the occurrence of *Pythium* root diseases of sorghum in the field is not well documented or understood. Many reports prior to 1973 of *Pythium* spp. causing root diseases of sorghum are erroneous or misleading due to the isolation and study of saprophytes from diseased tissue, the use of different species concepts by investigators, and evaluation of pathogenicity by inoculating sorghum with isolates from other host plants.

P. arrhenomanes Drechsler was first described as a pathogen of

0031-949X/80/08076606/$03.00/0

sorghum in 1937, when it was considered to be the causal organism in the very severe "milo disease" (2,9,15,21,39). Additional reports further described *P. arrhenomanes* as the primary pathogen. In 1948 and later, however, *Periconia circinata* (Mangin) Sacc. was proven to be the primary pathogen and *P. arrhenomanes* was thereafter considered to be only a secondary invader of toxin-damaged root tissue (18,19,26,30).

P. arrhenomanes was also pathogenic to sorghum seedlings in studies of root browning of grasses in the northern Great Plains (31–34,37,38). However, the organism was never clearly associated with any disease of sorghum in the field beyond the seedling stage. Other reports of *P. arrhenomanes* associated with diseased sorghum in the field also apparently refer only to young seedlings (1,3,27).

Several reports implicated *P. graminicola* Subr. as a pathogen of sorghum. Isolates from other hosts were weakly pathogenic to sorghum (12,36). The growing of sorghum in field plots resulted in greater root rot due to *P. graminicola* in subsequent indicator plants (35). In one instance, root rot of sorghum seedlings in the field was attributed partly to *P. graminicola* (1). However, most reports of *P. graminicola* from sorghum are misleading due to differences in usage of species names. Sprague (32) initially followed Drechsler (4) in considering *P. arrhenomanes* and *P. graminicola* to be distinct, but he considered isolates of *P. graminicola* studied in Iowa (13) to be identical with those reported as *P. arrhenomanes* from North Dakota (32). Later, Sprague considered the two species synonymous and assigned all reports of *P. arrhenomanes* on sorghum (principally references to milo disease) to *P. graminicola* (33).

Other reports described the isolation of additional species (1,10,23,25) and unidentified isolates (5,14,22,23,25) of *Pythium* from diseased sorghum roots. Numerous species of *Pythium* also were reported to cause damping-off of sorghum seedlings (6,11,16,17,20,24,31,33,34). However, none of these species or isolates were shown to cause root disease in established crops of sorghum.

In 1972 and later years, extensive losses due to lodging occurred in mature grain sorghum in the High Plains of Texas (7,8). Lodging occurred only in plants with root rot, and an unidentified species of *Phythium*, consistently isolated from diseased roots, was highly virulent on greenhouse-grown sorghum seedlings (7).

The previous reports (7,8) suggest that a serious *Pythium* disease of sorghum may exist in Texas and other sorghum-growing states of the great plains. Therefore, this study was undertaken to identify species of *Pythium* associated with root rot of grain sorghum and to evaluate their pathogenicity to seedlings and mature plants.

MATERIALS AND METHODS

Isolation, identification, and storage of *Pythium* isolates. In all isolation and reisolation attempts, portions of diseased root or stalk tissue up to 1.0 cm long were surface-sterilized in 1.0% sodium hypochlorite, rinsed in sterile distilled water, blotted on sterile filter paper, and plated on cornmeal agar (CMA) plus pimaricin (20 mg/L). Portions of colonies from isolation plates were grown through water agar and subsequently transferred to potato dextrose agar to confirm asepsis. Duplicate cultures of isolates were stored on CMA slants at 25 C and 4 C and transferred periodically (1–6 mo).

Pythium isolates were identified by characteristics of sexual structures formed on CMA, and by sporangia and zoospores formed on infested grass blades in water (40), according to the key of Waterhouse (40) and by reference to original (41) and secondary (4,28,42,43) species descriptions.

Infestation of soil and inoculation of plants. Infested cornmeal-sand mixture was added to soil prior to planting to evaluate damping-off of seedlings by the *Pythium* spp. Mixtures of cornmeal (4.5 g), sand (187 g), and water (50 ml) were autoclaved in 250-ml flasks, inoculated with infested agar blocks from cultures of individual isolates, and shaken every 3 days for 2 wk during incubation at 25 C. For each *Pythium* sp., cornmeal-sand inoculum of two or three isolates was composited. Inoculum was then mixed with soil (sandy clay loam sieved through a five meshes per cm screen) to give a 1:10 (v/v) concentration, and also diluted serially to 1:100 and 1:1,000. Soil in controls received noninfested cornmeal-sand. Cups (178 ml, 6-ounce) containing infested or control soil were each planted with 15 seeds of a sorghum inbred (Tx 412) and watered to saturation initially and at 4-day intervals for 3 wk at 25 C. Numbers of seedlings emerged were counted at 7 days, and numbers of plants killed were counted at 3 wk.

Inoculum of agar colonies comminuted in water was added to the soil around the roots of established plants. Cornmeal agar from three petri plates with *Pythium* grown 10 days at 25 C was cut into small sections (3–5 mm) and blended for 5 sec in 150 ml of distilled water. Inoculum from two or three isolates of each *Pythium* sp. was composited, and 15 ml was poured into a center-well formed in the soil of each pot (178 or 500 ml capacity) which contained three plants grown for 2, 4, or 8 wk. With mature (flowering to hard dough stage) plants, 50 ml of inoculum were poured into each of five wells surrounding a single plant in a 7.56-L (2-gallon) pot. Soil in pots with control plants received noninfested CMA.

Plants inoculated at 2, 4, or 8 wk of age were maintained at 23–27 C in combined Gro-Lux fluorescent and incandescent light (approximately 3,000 lx, 16-hr photoperiod) before and after inoculation. Plants inoculated at maturity were grown and maintained out-of-doors. Pots were watered every 2 days with drainage unimpeded or flooded with bottom dishes and drained at 2-day intervals.

Stalks of mature plants were inoculated with infested toothpicks or agar blocks (one of either per plant). Melted CMA was poured over toothpicks autoclaved in glass plates. After 2 days, toothpicks with agar coating were aseptically transferred to plates of CMA containing growing *Pythium* colonies and incubated for 7–8 days. Infested toothpicks were inserted into holes bored in lower nodes of stalks after leaf sheaths were removed. In other tests, agar blocks (2 cm^2) from the margins of growing colonies on CMA were placed over wounded nodes slashed 0.5 cm deep with a knife and the wounds were sealed with masking tape. Control plants received noninfested agar-coated toothpicks and agar blocks.

Evaluation of root and stalk rot. Plants inoculated at 2, 4, and 8 wk were maintained for an additional 2 wk. Mature inbred plants

TABLE 1. Pre-emergence and postemergence damping-off of sorghum seedlings incited by three species of *Pythium* in soil artificially infested at three inoculum levels

		Disease incidence and soil condition[z]			
		Pre-emergence damping-off (%)		Postemergence damping-off (%)	
Inoculum level[y]	*Pythium* species	Autoclaved soil	Natural soil	Autoclaved soil	Natural soil
High	0 (control)	15 a	28 ab	31 a	17 a
	P. periplocum	23 a	16 a	14 a	3 a
	P. myriotylum	74 b	43 b	73 b	45 b
	P. graminicola	71 b	75 c	81 b	19 ab
Intermediate	0 (control)	16 a	44 a	30 a	12 a
	P. periplocum	20 a	31 a	30 a	16 a
	P. myriotylum	27 a	27 a	74 b	47 b
	P. graminicola	47 b	27 a	83 b	54 b
Low	0 (control)	20 a	27 a	40 a	22 a
	P. periplocum	19 a	28 a	40 a	23 a
	P. myriotylum	8 a	21 a	82 b	65 b
	P. graminicola	22 a	19 a	91 b	42 ab

[y] Infested cornmeal-sand medium was mixed with soil and serially diluted to give ratios of 1/10 (high inoculum level), 1/100 (intermediate), and 1/1,000 (low) (v/v). Control soil received noninfested cornmeal-sand.

[z] Values are means of percentage damping-off in five pots (15 seeds planted per pot) as determined from emergence of seedlings (pre-emergence damping-off) 7 days after planting and survival of emerged seedlings (postemergence damping-off) 21 days after planting. Means within a column for each inoculum level not followed by the same letter differ significantly ($P = 0.05$) according to Duncan's multiple-range test.

were maintained for 4 wk following inoculation, and mature hybrids were maintained for 7 wk. Roots were then washed free of soil, and sizes of root masses (composited root systems) from individual pots with infested soil were estimated by visual comparisons with the mean root mass of the five corresponding control pots. Visual estimates gave less variation between replicate pots than did dry weight measurements because weights often were influenced by particles of soil and organic matter bound among roots. To reisolate *Pythium* spp., three-to-five sections of rotten or discolored roots were excised from root masses of each group of inoculated plants, surface-sterilized, and plated.

TABLE 2. Sizes of root systems of sorghum plants of different ages grown in soil artificially infested with three species of *Pythium*

Age of plants when soil was infested (wk)[y]	*Pythium* species	Soil condition and sizes of root systems as percentages of controls[z]	
		Autoclaved soil	Natural soil
2	*P. graminicola*	25 a	83 a
	P. myriotylum	87 b	83 a
	P. periplocum	68 b	71 a
4	*P. graminicola*	28 a	49 a
	P. myriotylum	52 a	75 a
	P. periplocum	72 a	80 a
8	*P. graminicola*	53 a	98 a
	P. myriotylum	111 b	105 a
	P. periplocum	93 b	98 a

[y]To infest soil, comminuted agar cultures were poured into centerwells in pots and covered with soil. Control pots received noninfested agar.

[z]Values are means of sizes of composited root systems of three plants from each of five pots expressed as percentages of the mean control size. Estimates of sizes were determined by visual observations 14 days after inoculation. Means within a column for each age which are not followed by the same letter differ significantly ($P = 0.05$) according to Duncan's multiple-range test.

Stalks of inoculated plants were bisected to determine whether pith tissue was rotted beyond immediate points of inoculation. Three-to-five pieces of tissue from margins of rotted pith in each diseased plant were surface-sterilized and plated.

RESULTS

Disease symptoms in the field and *Pythium* spp. isolations. *Pythium* spp. were isolated from mature sorghum plants with root rot in a nursery in north Texas, and from plants with apparent root rot and insect damage in a commercial field in southern Texas, in October 1976. Root rot in the nursery was most severe in entries selected for resistance to greenbug (*Schizaphis graminum*), and this sometimes resulted in lodging of 90–100% of plants. On plants in which large roots were not completely rotted, sunken red-brown to black lesions were present on outer tissue where fine roots emerged; these often coalesced and encircled and constricted roots. Tissue beneath lesions was usually white, but in roots rotted up to the stalks all tissues were uniformly tan. *Pythium* colonies developed from nearly all tissue pieces on CMA plus pimaricin, and 49 isolates were collected from 17 plants.

Plants in southern Texas were lodged in patches at the edge of an irrigation pattern. Most lodged plants had symptoms of root rot and also stalk damage caused by the southwestern corn borer (*Diatraea grandiosella*). Often symptoms were indistinguishable: borers sometimes penetrated into basal portions of large roots, and rotted tissue extended from roots into lower stalks adjacent to borer cavities. Diseased roots were uniformly tan, without external lesions, and frequently hollow or rotted internally with epidermal tissues intact. *Pythium* colonies developed from plated tissue of only two of 11 plants, but they originated from both root and stalk tissue in each plant. Ten isolates were obtained.

Identities and characteristics of *Pythium* isolates. The 49 isolates from north Texas were identified as *P. graminicola*. Eight isolates from south Texas were identified as *P. periplocum*

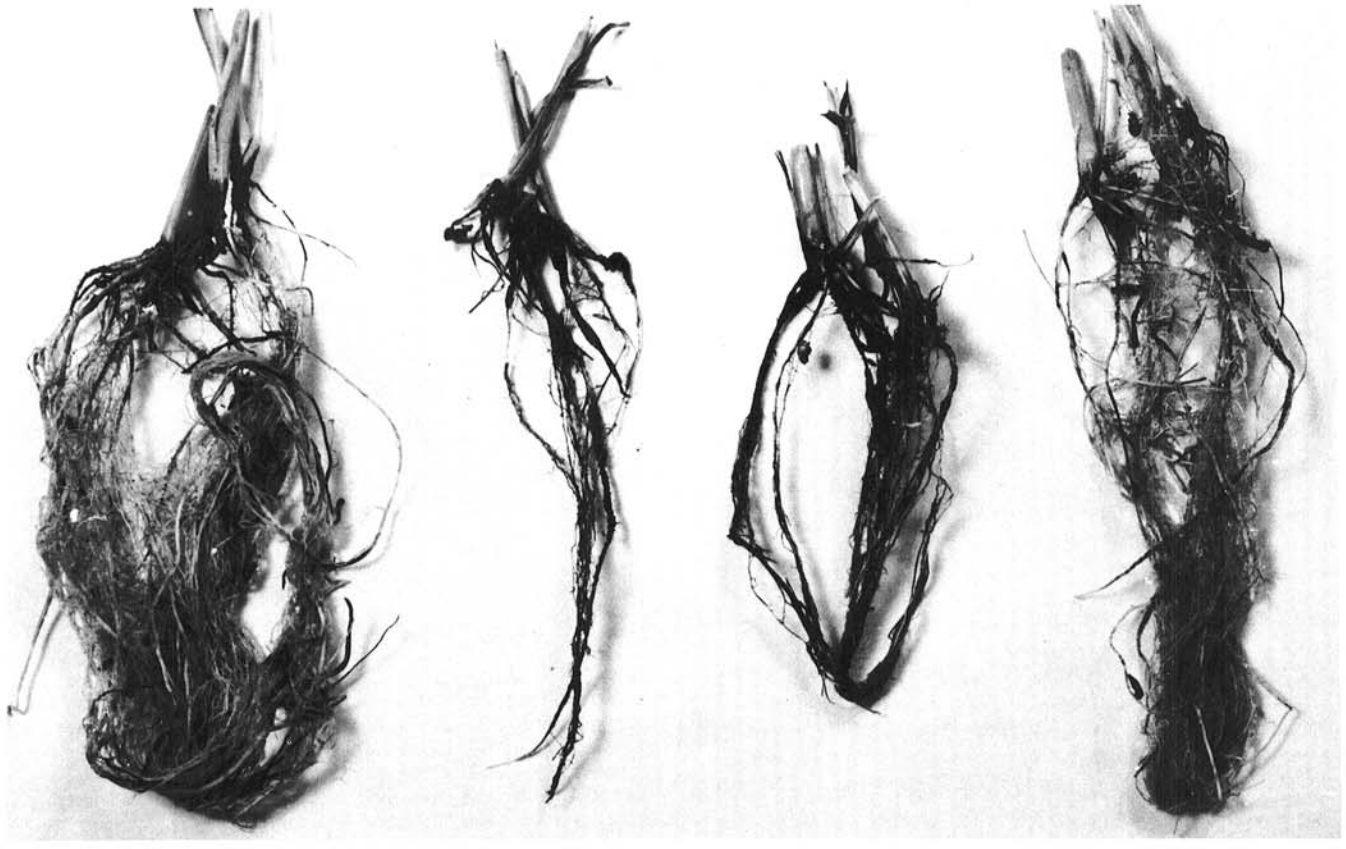

Fig. 1. Sizes of composited root systems of three 6-wk-old sorghum seedlings following growth in autoclaved soil (left to right) noninfested, and infested with *Pythium graminicola, P. myriotylum,* and *P. periplocum.*

Drechsler, and the remaining two were identified as *P. myriotylum* Drechsler.

Most isolates of *P. graminicola* produced few-to-numerous lobulate sporangia on surfaces of colonies on CMA, and these appeared macroscopically as dense tufts of white mycelium. Sporangia also were abundant on colonies grown from grass blades after 2 days in distilled or soil-extract water. When such colonies were transferred to 4 C for 1 hr and subsequently rinsed in distilled water three times at 0.5-hr intervals, numerous zoospores were released after an additional 2 hr. Tubes attached to vesicles were traced back to emptied lobulate sporangia. Few-to-numerous oogonia and oospores were observed in 35 isolates, and none were observed in 14 isolates. Wherever sexual structures were produced in colonies, sporangia were absent and vice versa. Antheridia were monoclinous and diclinous, swollen, and made broad apical contact with oogonia; two antheridia were applied to the majority of oogonia which developed oospores, and one or three were present on the remainder. Oospores were thickwalled and nearly always plerotic; walls were pale lavender and inner contents were light yellow or gold. Mean oogonial diameters of some isolates were less than 25 μm, which Waterhouse (40) considered a minimal size for *P. graminicola.*

When five isolates which produced no sexual structures in single culture were crossed in all combinations on CMA, either none or few-to-very-numerous oogonia and oospores developed in heterothallic mating reactions in various crosses. The oogonia were present in patches or throughout the agar, and in one or both crossed thalli. Macroscopically visible mating reactions were never observed with isolates of *P. graminicola.* Asexual isolates also produced numerous oospores in some crosses with weakly homothallic isolates.

Characteristics of *P. myriotylum* isolates were similar to those previously described, except that sizes of oogonia (average 30.0 μm in diameter) were closer to those reported for *P. arrhenomanes* than for *P. myriotylum* (40,41,43). *P. periplocum* isolates were identical to those described by Drechsler (41) except that mean diameters of oogonia and oospores (20 and 18 μm, respectively) of the Texas isolates were slightly smaller.

Damping-off and root rot of inbred plants. *P. graminicola* and *P. myriotylum* caused both pre-emergence and postemergence damping-off of seedlings of the sorghum inbred, whereas *P. periplocum* did not cause significant damping-off under any conditions (Table 1). Pre-emergence damping-off by *P. graminicola* and *P. myriotylum* was most severe in autoclaved soil at the highest inoculum level. Only *P. graminicola* significantly reduced emergence in field soil or at the intermediate inoculum level. Postemergence damping-off, in contrast, was generally similar for the two species in both autoclaved and field soil and at all inoculum levels.

In plants inoculated at 2, 4, and 8 wk of age, *P. graminicola* usually caused more severe disease than did *P. myriotylum* and *P. periplocum* in autoclaved soil, but not in untreated field soil (Table 2, Fig. 1). The latter two species caused similar disease in both soils. Periodic flooding of soil decreased sizes of root masses to a similar extent in both control and infested pots and therefore did not result in noticeably greater disease. In all experiments, plants inoculated with *P. graminicola* had the greatest number of lesions on roots and the most visibly rotted roots, while those inoculated with *P. myriotylum* had fewer lesions and rotted roots. Few lesions were visible on roots of plants inoculated with *P. periplocum. P. graminicola* was reisolated from plated root tissue of all plants assayed. *P. myriotylum* was reisolated from at least 67% of plants of all ages, but *P. periplocum* was reisolated from no more than 10% of plants of any age.

To evaluate pathogenicity of the *Pythium* spp. to mature inbred plants, inoculum of each species was added to soil surrounding five plants at the milk or soft dough stage. Soil was flooded and drained at alternate 2-day intervals for 4 wk. Sizes of root masses of plants from infested soil did not differ from controls in this experiment. However, plants inoculated with *P. graminicola* had red-brown, constricted lesions on large roots which sometimes extended to crowns. Zones between rotted and healthy tissue were sharply defined in cross section. Plants inoculated with *P. myriotylum* had fewer lesions on large roots and the lesions never extended to crowns. No lesions were apparent on large roots of plants grown in soil infested with *P. periplocum.*

P. graminicola was reisolated from three to five of the plants inoculated at maturity, *P. myriotylum* from one plant, and *P. periplocum* was not reisolated.

Resistance and susceptibility to root rot induced by *P. graminicola* was evaluated in plants of four experimental sorghum hybrids at 2 wk of age and at flowering. Two hybrids (Tx 399 × Tx 2567 and Tx 413 × TAM 2568) were resistant to greenbug and two (Tx 399 × Tx 2536 and Tx 378 × Tx 2536) were susceptible. No differences in susceptibility between the hybrids were evident in 2-wk-old plants. Mean sizes of root masses from five infested pots of each hybrid were 38–47% of the mean control size in autoclaved soil and 66–85% of that in untreated field soil. However, among five plants of each hybrid inoculated at flowering, sizes of root systems were significantly reduced ($P = 0.05$) in all plants of Tx 413 × TAM 2568 (mean = 30% of control size) (Fig. 2) but not in those of the other three hybrids. In plants of the second greenbug-resistant hybrid, root systems from infested pots were similar in size to those from control pots. *P. graminicola* was reisolated from all plants of the hybrid with severe root rot, but only from one or two plants of each of the other three hybrids.

Stalk inoculations. Stalks of inbred plants grown in pots and the four hybrids grown in a field nursery were inoculated at maturity with toothpicks and agar blocks infested with the *Pythium* spp. No stalk rot developed in any inbred plants following inoculation. However, in 13 of 120 hybrid plants inoculated with *P. gramincola* by both methods, including one or more from each hybrid, a slight to extensive light-brown stalk rot developed. Pith tissue was distintegrated, leaving vacular bundles exposed (Fig. 3), and white mycelia with coenocytic hyphae were sometimes visible in rotted areas. Symptoms were identical in the 13 plants, but *P. graminicola* was reisolated from margins of rotted pith of only two plants. This low frequency of reisolation was attributed to extensive disintegration of rotted pith tissue during surface-sterilization and plating.

DISCUSSION

Results of this study demonstrate that *P. graminicola* is a virulent pathogen of both seedlings and mature plants of grain sorghum. Symptoms that developed in mature plants inoculated

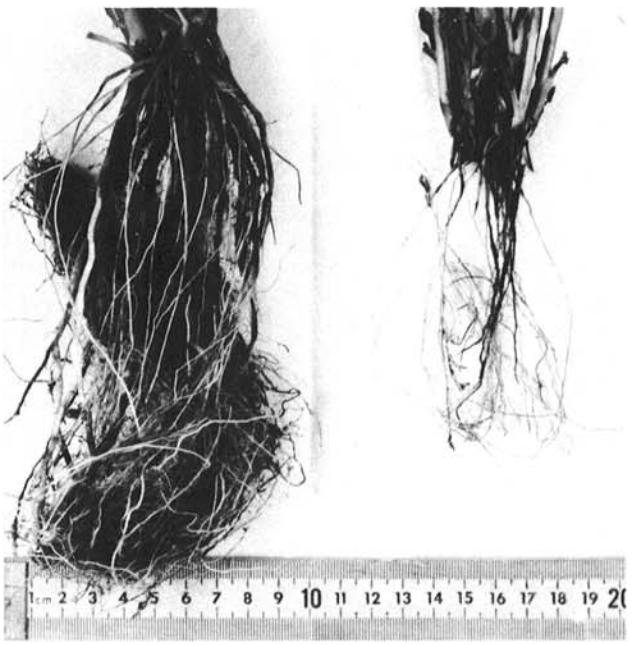

Fig. 2. Sizes of root systems of two plants of a sorghum hybrid following growth in pots and addition of noninfested agar (left) and agar infested with *Pythium graminicola* (right) to soil at flowering. Scale is in centimeters.

with *P. graminicola* (Fig. 2) were similar to those observed in the field, where symptoms of the milo disease caused by *P. circinata* (9,15,21) were not present. These observations and results justify the concept of a *Pythium* root disease of sorghum (8) that causes losses in mature stands due to destruction of roots and subsequent lodging of stalks.

P. graminicola is likely the principal causal organism of Pythium root rot of sorghum. It comprised 100% of isolates obtained from a nursery with severe disease and was the most virulent of the three species tested. Symptoms and severity of disease caused by *P. graminicola* in the field were generally similar to those reported in epidemics which occurred earlier in the same area (7,8). This suggests that the same disease was observed in both instances.

P. myriotylum, although less virulent than *P. graminicola*, caused some damage to seedlings and mature plants in most experiments, and it was isolated from diseased plants in a field where *P. graminicola* was not found. Possibly this and other *Pythium* spp. also may cause root disease, especially when plants are predisposed by other agents. Root rot in plants from which *P. myriotylum* was isolated was closely associated with stalk borer damage which in itself greatly weakened plants. *P. periplocum*, in contrast, was only slightly virulent and probably had been present only as a saprophytic invader of damaged tissue.

P. graminicola does not appear to be a stalk rot pathogen of sorghum in Texas. In plants naturally infected in the field, rotting of tissue occurred throughout root systems, but never extended up into stalks, and lodging always resulted from breakage at the soil line. However, stalk rot did develop in a small percentage of plants inoculated in a nursery, and *P. graminicola* was reisolated from margins of rotted pith. This form of the disease might occur in other sorghum-growing areas with different environmental conditions.

Resistance to Pythium root rot apparently occurs in many sorghum lines and hybrids. Only a minority of entries in a nursery had plants lodged due to root rot and these were mainly greenbug-resistant lines. However, although one such line tested in this study was highly susceptible to *P. graminicola* at maturity, another was resistant, which indicates that susceptibility to Pythium root rot is not always correlated with greenbug resistance.

P. graminicola and *P. arrhenomanes* are morphologically similar species which appear to have been confused in many previous reports. Subramanian (41) described *P. graminicola* as a species with thickwalled plerotic oospores and one-to-three clavate, often monoclinous antheridia which were broadly applied to oogonia. Drechsler (41) described *P. arrhenomanes* with primarily alperotic oospores and numerous antheridia (often 15–20 or more) which often arose from branched hyphae and made narrow contact with oogonia. He later described additional features of *P. arrhenomanes* to distinguish it from *P. graminicola* (4). Rands and Dopp (28) compared numerous isolates of *P. arrhenomanes* and concluded that while many had fewer antheridia (four-to-ten) than those originally described by Drechsler, all were of the same species because antheridia were characteristically diclinous, crook-necked, narrowly applied to oogonia in a radiate pattern, and often arose as multiple branches from a single hypha.

The 49 isolates from sorghum that were identified as *P. graminicola* in this study conform closely to original (41) and secondary (4,25,42) descriptions of that species in that oospores are consistently plerotic and thick-walled, and antheridia are few (one-to-three), clavate, often monoclinous, and broadly applied to oogonia. These features also clearly distinguish the sorghum isolates from *P. arrhenomanes* (4,25,28,41,43). Therefore, these observations do not support Sprague's view of synonymy of the species. Middleton (25), Waterhouse (40), and Waterhouse and Waterston (42,43) also considered *P. arrhenomanes* and *P. graminicola* to be distinct. However, we do agree with Sprague (32) that some or all of the isolates described as *P. graminicola* from Iowa are in fact *P. arrhenomanes* based upon their aplerotic oospores and branched antheridia which are usually applied as four per oogonium (13). The apparent error in identification of species in Iowa, or the possible study of mixed isolates and populations of both species, precludes comparisons between results obtained there and in other studies of *P. graminicola* (29). These differences in usage of species names and concepts clearly point to the need for morphological descriptions to accompany species names in future reports on *P. graminicola, P. arrhenomanes,* and related *Pythium* spp.

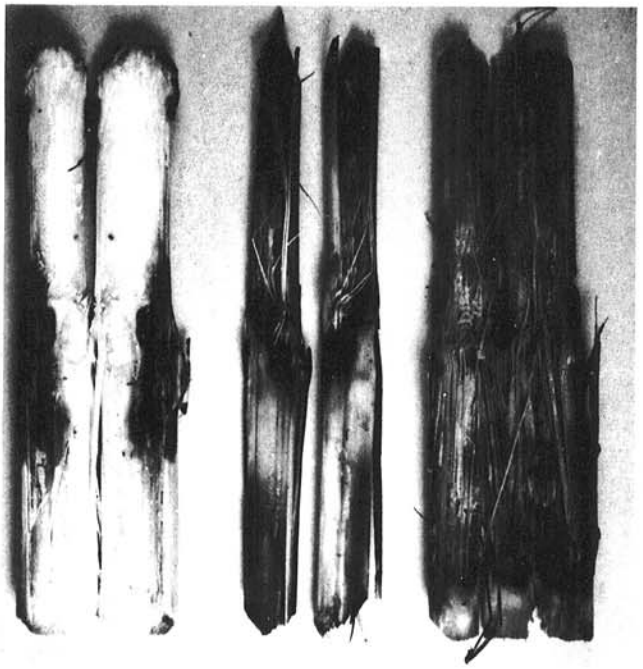

Fig. 3. Bisected stalks of plants of a sorghum hybrid grown in a nursery and inoculated with agar blocks taped over wounds on nodes. Plant on left received noninfested agar, plants on right received agar infested with *Pythium graminicola.*

LITERATURE CITED

1. BALDOVINAS de La PEÑA, G., and R. GARZA-CHAPA. 1963. Aspectos fitopatologicas sobresalientes de las plantas de sergo cultivado en Mexico y sedidas cuarentenarias pertinentes. Rev. Tec. Col. Ing. Agron. Mex. 5:37-45. (Rev. Appl. Mycol. 46:185).
2. BOWMAN, D. H., J. H. MARTIN, L. E. MELCHERS, and J. H. PARKER. 1937. Inheritance of resistance to Pythium root rot in sorghum. J. Agric. Res. 55:105-115.
3. CICCARONE, A., and J. T. MIDDLETON. 1951. Two species of *Pythium* recorded from Venezuela. Plant Dis. Rep. 35:387.
4. DRECHSLER, C. 1936. *Pythium graminicolum* and *P. arrhenomanes.* Phytopathology 26:676-684.
5. DYER, R. A. 1951. Plant classification and control of crop diseases. Farming in South Africa 26:488-490. (Rev. Appl. Mycol. 31:536).
6. EDGERTON, C. W., E. C. TIMS, and P. J. MILLS. 1929. Relation of species of *Pythium* to the root-rot disease of sugarcane. Phytopathology 19:549-564.
7. EDMUNDS, L. K., R. L. VOIGT, R. A. FREDERIKSEN, and L. D. DUNKLE. 1973. Root and stalk rot problems in the Great Plains. Pages 82–92 in: Proc. 8th Bienn. Grain Sorghum Res. and Util. Conf., 27 February–1 March 1973, Lubbock, TX.
8. EDMUNDS, L. K., and N. ZUMMO. 1975. Sorghum diseases in the United States and their control. U.S. Dept. Agric., Handb. 468. 47 p.
9. ELLIOTT, C., L. E. MELCHERS, C. L. LeFEBVRE, and F. A. WAGNER. 1937. Pythium root rot of milo. J. Agric. Res. 54:797-834.
10. FISCHER, G. W., R. SPRAGUE, H. W. JOHNSON, and J.R. HARDISON. 1942. Host and pathogen indices to the diseases observed on grasses in certain western states during 1941. Plant Dis. Rep. Suppl. 137:87-144.
11. FREEMAN, T. E., H. H. LUKE, and D. T. SECHLER. 1966. Pathogenicity of *Pythium aphanidermatum* on grain crops in Florida. Plant Dis. Rep. 50:292-294.
12. HO, W.-C. 1938. *Pythium graminicola* on barley in Iowa. (Abstr.) Phytopathology 28:9.
13. HO, W.-C., C. H. MEREDITH, and I. E. MELHUS. 1941. *Pythium graminicola* Subr. on barley. Iowa Agric. Exp. Stn. Res. Bull. 287:289-314.
14. HOFFMASTER, D. E. 1942. The sorghum root-and-stalk rot complex

in Oklahoma. (Abstr.) Phytopathology 32:9.
15. KENDRICK, J. B., and F. W. BRIGGS. 1939. Pythium root rot of milo and the development of resistant varieties. Calif. Agric. Exp. Stn. Bull. 629:1-18.
16. KRIETLOW, K. W., R. J. GARBER, and R. R. ROBINSON. 1950. Investigations on seed treatment of alfalfa, red clover, and sudan grass for control of damping-off. Phytopathology 40:883-898.
17. LEUKEL, R. W. 1943. Chemical seed treatments for the control of certain diseases of forages. U.S. Dep. Agric., Tech. Bull. 849. 24 pp.
18. LEUKEL, R. W. 1948. *Periconia circinata* and its relation to milo disease. J. Agric. Res. 77:201-222.
19. LEUKEL, R. W., and A. G. JOHNSON. 1948. *Periconia circinata*, the cause of milo disease. Science 107:93-94.
20. LEUKEL, R. W., and J. H. MARTIN. 1943. Seed rot and seedling blight of sorghum. U.S. Dep. Agric., Tech. Bull. 839. 26 pp.
21. LEUKEL, R. W., J. H. MARTIN, and C. L. LeFEBVRE. 1944. Sorghum diseases and their control. U.S. Dep. Agric. Farmer's Bull. 1959. 46 pp.
22. LYON, H. L. 1936. Botany, forestry and pathology. Pages 26–37 in: Proc. Hawaiian Sugar Planters' Assoc. 1935. (Rev. Appl. Mycol. 15:559).
23. MARTIN, J. R. 1937. Pathology. Pages 28–35 in: Proc. Hawaiian Sugar Planters' Assoc. 1936. (Rev. Appl. Mycol. 16:561).
24. McCARTER, S. M., and R. H. LITTRELL. 1970. Comparative pathogenicity of *Pythium aphanidermatum* and *Pythium myriotylum* to twelve plant species and intraspecific variation in virulence. Phytopathology 60:264-268.
25. MIDDLETON, J. T. 1943. The taxonomy, host range, and geographic distribution of the genus *Pythium*. Mem. Torrey Bot. Club 20:1-171.
26. ODVODY, G. N., L. D. DUNKLE, and L. K. EDMUNDS. 1977. Characterization of the *Periconia circinata* population in a milo disease nursery. Phytopathology 67:1485-1489.
27. PADWICK, G. W. 1956. Losses caused by plant diseases in the colonies. Commonw. Mycol. Inst., Phytopathol. Pap. 1. 60 pp.
28. RANDS, R. D., and E. DOPP. 1934. Variability in *Pythium arrhenomanes* in relation to root rot of sugarcane and corn. J. Agric. Res. 49:189-221.
29. RAO, B., A. F. SCHMITTHENNER, R. CALDWELL, and C. W. ELLET. 1978. Prevalence and virulence of *Pythium* species associated with root rot of corn in poorly drained soil. Phytopathology 68:1557-1563.
30. SCHEFFER, R. P., and R. B. PRINGLE. 1961. A selective toxin produced by *Periconia circinata*. Nature 191:912-913.
31. SPRAGUE, R. 1943. Root rots of graminae in the northern Great Plains, 1940–1943. Plant Dis. Rep. 27:248-250.
32. SPRAGUE, R. 1944. Root rots of cereals and grasses in North Dakota. N. Dakota Agric. Exp. Stn. Bull. 332. 35 pp.
33. SPRAGUE, R. 1950. Diseases of Cereals and Grasses in North America. Ronald Press, New York, NY. 538 pp.
34. SPRAGUE, R., and R. E. ATKINSON. 1942. Cross inoculation with *Pythium arrhenomanes* from cereals and grasses in the northern great plains. (Abstr.) Phytopathology 32:17.
35. STAUDINGER, W. L., and W. F. BUCHHOLTZ. 1965. Effect of two legume and two grass crop root systems on *Pythium graminicolum* disease inciting potential of field soil. Iowa State Coll. J. Sci. 39:453-458.
36. SUBRAMANIAN, L. S. 1936. Some new seedling diseases of sugarcane. Indian J. Agric. Sci. 6:11-16 (Rev. Appl. Mycol. 15:465).
37. VANTERPOOL, T. C. 1940. Present knowledge of browning root rot of wheat with special reference to its control. Sci. Agric. 30:735-749.
38. VANTERPOOL, T. C., and R. SPRAGUE. 1942. *Pythium arrhenomanes* on cereals and grasses in the northern Great Plains. Phytopathology 32:327-328.
39. WAGNER, F. A. 1936. Reaction of sorghum to the root, crown, and shoot rot of milo. Agron. J. 28:643-654.
40. WATERHOUSE, G. M. 1967. Key to *Pythium* Pringsheim. Mycol. Paper 109. Commonw. Mycol. Inst., Assoc. Appl. Biologists, Kew, Surrey, England. 15 pp.
41. WATERHOUSE, G. M. 1968. The genus *Pythium* Pringsheim. Mycol. Paper 110. Commonw. Mycol. Inst., Assoc. Appl. Biologists, Kew, Surrey, England. 50 pp.
42. WATERHOUSE, G. M., and J. M. WATERSTON. 1964. *Pythium graminicola*. No. 38 in: Description of plant pathogenic fungi and bacteria. Commonw. Mycol. Inst., Assoc. Appl. Biol., Kew, Surrey, England. 2 pp.
43. WATERHOUSE, G. M., and J. M. WATERSTON. 1964. *Pythium arrhenomanes*. No. 39 in: Description of plant pathogenic fungi and bacteria. Commonw. Mycol. Inst., Assoc. Appl. Biologists, Kew, Surrey, England. 2 pp.