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Reproduction of *Belonolaimus longicaudatus, Meloidogyne javanica, Paratrichodorus minor,* and *Pratylenchus brachyurus* on Pearl Millet (*Pennisetum glaucum*)

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Abstract: Pearl millet (*Pennisetum glaucum*) has potential as a grain crop for dryland crop production in the southeastern United States. Whether or not pearl millet will be compatible in rotation with cotton (*Gossypium hirsutum*), corn (*Zea mays*), and peanut (*Arachis hypogaea*) will depend, in part, on its host status for important plant-parasitic nematodes of these crops. The pearl millet hybrid 'TifGrain 102' is resistant to both *Meloidogyne incognita* race 3 and *M. arenaria* race 1; however, its host status for other plant-parasitic nematodes was unknown. In this study, the reproduction of *Belonolaimus longicaudatus, Paratrichodorus minor, Pratylenchus brachyurus,* and *Meloidogyne javanica* race 3 on pearl millet ('HGM-100' and TifGrain 102) was compared relative to cotton, corn, and peanut. Separate greenhouse experiments were conducted for each nematode species. Reproduction of *B. longicaudatus* was lower on peanut and the two millet hybrids than on cotton and corn. Reproduction of *P. minor* was lower on peanut and TifGrain 102 than on cotton, corn, and HGM-100. Reproduction of *P. brachyurus* was lower on both millet hybrids than on cotton, corn, and peanut. Reproduction of *M. javanica* race 3 was greater on peanut than on the two millet hybrids and corn. Cotton was a nonhost. TifGrain 102 was more resistant than HGM-100 to reproduction of *B. longicaudatus, P. minor,* and *M. javanica.* Our results demonstrated that TifGrain 102 was a poor host for *B. longicaudatus* and *P. brachyurus* (Rf < 1) and, relative to other crops tested, was less likely to increase densities of *P. minor* and *M. javanica.*

Key words: Arachis hypogaea, Belonolaimus longicaudatus, corn, cotton, *Gossypium hirsutum,* lesion nematode, *Meloidogyne javanica, Paratrichodorus minor,* peanut, pearl millet, *Pennisetum glaucum, Pratylenchus brachyurus,* reproduction, resistance, root-knot nematode, sting nematode, stubby-root nematode, *Zea mays.*

In the United States, pearl millet (*Pennisetum glaucum*) traditionally has been grown as a summer annual forage crop. However, there is growing interest in pearl millet as alternative feed grain in poultry diets (Adeola et al., 1994; Davis et al., 2003; Smith et al., 1989b). Parental inbreds have been developed, making possible the production of pearl millet grain hybrids adapted to the environment and crop production practices of the southern United States (Hanna, 1993; Hanna et al., unpubl. data). Hybrids adapted to this region are dwarf, high yielding, resistant to the rust fungus, *Puccinia substriata* var. *indica,* and early maturing. In addition, pearl millet is drought tolerant and resistant to pre-harvest aflatoxin contamination; thus, it is suitable for dryland crop production (Payne et al., 1990; Smith et al., 1989a; Wilson et al., 1995).

Grain hybrids of pearl millet are likely to be grown in rotation with other field crops. In the southeastern United States (Alabama, Florida, Georgia, and South Carolina), cotton (*Gossypium hirsutum*), corn (*Zea mays*), and peanut (*Arachis hypogaea*) are the predominant field crops. The average number of hectares planted in this region from 2000 to 2003 was 974,700 for cotton, 405,900 for corn (grain and silage), and 332,300 for peanut (USDA, National Agricultural Statistics Service, n.d.). These crops are grown frequently in rotation with each other to suppress soil-borne diseases and plant-parasitic nematodes. Whether or not pearl millet will be compatible in rotation with other field crops will depend, in part, on its host status for important plant-parasitic nematodes of these crops.

Meloidogyne spp. are the most widespread and damaging plant-parasitic nematodes of field crops (Sasser and Carter, 1985). Pearl millet is a host for these nematodes; however, hybrids vary in their susceptibility (Johnson et al., 1977). The grain hybrid 'HGM-100' was susceptible to both *Meloidogyne incognita* race 3 and *M. arenaria* race 1, whereas grain hybrids with either 114 or 117 (= 'Tift 454' inbred) as the male pollinator were resistant (Timper et al., 2002). The resistance to *M. incognita* and *M. arenaria* in the recently released grain hybrid 'TifGrain 102' comes from Tift 454 (Hanna et al., unpubl. data). *Belonolaimus longicaudatus* is extremely damaging to cotton and corn throughout the Southeast, and to peanut in North Carolina and Virginia (Dickson, 1998; Perry and Rhoades, 1982). However, the distribution of this nematode is limited to very sandy soils. Pearl millet has also been reported to be a good host for *B. longicaudatus* (Johnson and Burton, 1973; Robbins and Barker, 1973). *Paratrichodorus minor* has a broad host range and is widespread in the southeastern United States (Perry and Rhoades, 1982). Both corn and cotton are good hosts for this nematode, but only corn is reported to be damaged by *P. minor* (Koenning et al., 1999; Perry and Rhoades, 1982; Rohde and Jenkins, 1957; Schilt and Cohn, 1975). Peanut and pearl millet were poor or nonhosts for *P. minor* (Baujard and Martiny, 1995). *Pratylenchus brachyurus* reproduces in roots of corn, cotton, peanut, and pearl millet; however, damage from this nematode has been reported only in peanut (Thames, 1982).

Although pearl millet is known to support reproduction of *B. longicaudatus, M. javanica, P. minor,* and *P.*

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brachyurus, the host status of two grain hybrids, HGM-100 and TifGrain 102, was unknown. Moreover, few studies have compared reproduction of these nematodes on pearl millet relative to other known host and nonhost plants. Therefore, the objective of this study was to compare reproduction of these four plant-parasitic nematodes on pearl millet relative to cotton, corn, and peanut. In a previous study, we compared reproduction of *M. incognita* race 3 and *M. arenaria* race 1 on grain hybrids of pearl millet relative to field corn hybrids (Timper et al., 2002).

Materials and Methods

Nematode inoculum: Belonolaimus longicaudatus was isolated from corn in Tift County, Georgia, and cultured on bermudagrass (*Cynodon dactylon* cv. Cheyenne). *Paratrichodorus minor* was isolated from tall fescue (*Festuca arundinacea* cv. Jesup) in Clarke County, Georgia, and cultured on the same host. Inoculum of *B. longicaudatus* and *P. minor* was extracted from soil using centrifugal flotation (Jenkins, 1964). *Meloidogyne javanica* race 3 was isolated from peanut in Texas (provided by J. L. Starr, Texas A&M, College Station, TX) and cultured alternately on tomato (*Lycopersicon esculentum* cv. Rutgers) and peanut cv. Georgia Green. Eggs for inoculum were collected from roots of tomato using 0.5% NaOCl (Hussey and Barker, 1973). *Pratylenchus brachyurus* was isolated from peanut in Tift County, Georgia, and cultured on the corn hybrid 'Pioneer 3223'. Inoculum was obtained by placing infected corn roots in a mist chamber for 4 to 7 days. Nematodes were collected from the mist chamber every 2 days and stored at 5 °C for no more than 1 week before inoculation.

Nematode reproduction on different crops: Separate experiments were conducted for each nematode species. Experiments were conducted in 15-cm-diam. plastic pots containing 2,700 cm^3 of a loamy sand (82% sand, 9% silt, 7% clay, 1% organic matter; pH 5.3). The two pearl millet hybrids, HGM-100 and TifGrain 102, were planted at 5 seeds/pot 1 week before the other crops. Corn (Pioneer 3223), cotton ('DP 5415'), and peanut ('Georgia Green') were planted at 2 seeds/pot. All crops were thinned to 1 plant/pot. Each pot was inoculated 2 to 3 weeks after planting with either juveniles and adults of *B. longicaudatus, P. minor,* and *P. brachyurus,* or with eggs of *M. javanica.* The inoculum was distributed between two holes (2 cm deep) at the base of each plant. The inoculation rates, number of replications, and duration of each experiment are summarized in Table 1. Crop treatments were completely randomized on a single greenhouse bench with soil temperatures ranging from 17 °C to 35 °C. Plants were fertilized at planting with a slow-release formulation (14-14-14, N-P-K) and watered as needed.

At the end of each experiment, *B. longicaudatus, P. minor,* and *P. brachyurus* were extracted by centrifugal flotation from 250 cm^3 of soil from each pot. For *P. brachyurus,* fresh root weights were determined and either the whole root system, or a 20- to 50-gram subsample of roots was placed on Baermann funnels in a mist chamber. Nematodes that migrated out of the roots after 1 week were counted. All counts were converted to total nematodes per pot, including those from roots and soil. Eggs of *M. javanica* were extracted from the entire root system by cutting the roots into ca. 5-cm pieces, placing them in a 1-liter flask, and agitating for 4 minutes in a 1% NaOCl solution. Eggs were collected and rinsed with tap water on nested 150- and 25-μm-pore sieves. Data were transformed by square root prior to statistical analysis. Analysis of variance was used to determine the effect of crop and experimental trial on nematode numbers, and Fisher's LSD test was used to determine differences among crops (SAS Institute, Cary, NC).

Table 1. Inoculum levels, number of replications, and duration of experiments for four species of nematodes.

Nematode	Expt.	Inoculum per pot	No. replicates	Duration of experiment (days)[a]
Belonolaimus longicaudatus	1	200	9	56
	2	199	9	63
Meloidogyne javanica	1	8,058	8	62
	2	8,073	8	60
Paratrichodorus minor	1	503	9	63
	2	502	8	63
Pratylenchus brachyurus	1	665	7	60
	2	462	6	61

[a] Number of days from inoculation to extraction of nematodes from roots and soil.

Results and Discussion

Belonolaimus longicaudatus: Reproduction of *B. longicaudatus* on the different crops was consistent between experiments; therefore, the combined data are presented. Final nematode numbers were greatest ($P \leq 0.05$) on cotton and corn, and least on peanut and TifGrain 102 pearl millet (Fig. 1). Among the two pearl millet hybrids, HGM-100 was a better ($P \leq 0.05$) host for *B. longicaudatus* than TifGrain 102. The reproductive factors (Rf = final numbers/initial numbers) for cotton, corn, and HGM-100 were 16.0, 13.6, and 2.4, respectively. Peanut and TifGrain 102 were poor hosts with Rf values of 0.3 and 0.6, respectively.

In the southern United States, populations of *B. longicaudatus* can differ in both morphological features and host range, suggesting the existence of either distinct species or races of this nematode (Abu-Gharbieh and Perry, 1970; Robbins and Barker, 1973; Robbins and Hirschmann, 1974). Robbins and Barker (1973) reported that a Georgia population differed in host range from three North Carolina populations; however,

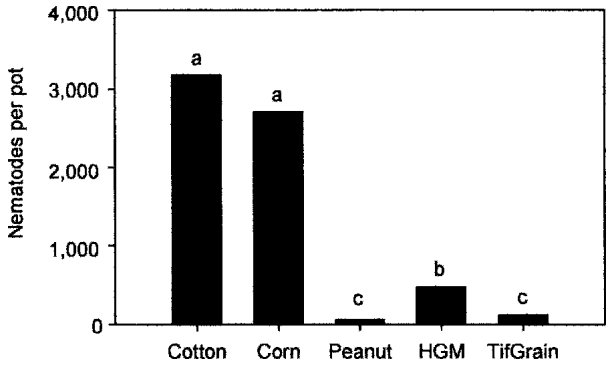

FIG. 1. Reproduction of *Belonolaimus longicaudatus* on cotton (*Gossypium hirsutum*), corn (*Zea mays*), peanut (*Arachis hypogaea*), and two pearl millet (*Pennisetum glaucum*) hybrids, HGM-100 and TifGrain 102. Bars are the mean of 18 replicates from two experiments, and those with the same letter are not different ($P > 0.05$) based on Fisher's LSD test.

all the populations reproduced on cotton, corn, peanut, and pearl millet. Our results support numerous other studies demonstrating high reproductive rates of *B. longicaudatus* on cotton and corn (Brodie et al., 1970a; Graham and Holdeman, 1953; Holdeman and Graham, 1953; Lautz, 1959; McSorley and Dickson, 1989; Rhoades, 1985; Robbins and Barker, 1973). In our study, Georgia Green peanut was a poor host for this nematode, whereas in several other studies, peanut was shown to be a good host (Rf > 2) for *B. longicaudatus* (Abu-Gharbieh and Perry, 1970; Holdeman and Graham, 1953; Lautz, 1959; Robbins and Barker, 1973). In a field study, Brodie et al. (1970) observed high populations of this nematode following cotton and corn but low populations following peanut, indicating peanut was a relatively poor host. These contradictory results may be due to differences among nematode populations or among peanut cultivars used in the studies. Resistance to *B. longicaudatus* in peanut has not been investigated thoroughly; nevertheless, peanut cultivars have been reported to vary in their ability to support reproduction of this nematode (Holdeman and Graham, 1953).

Some pearl millet hybrids are excellent hosts (Rf > 10) for *B. longicaudatus* (Johnson and Burton, 1973; Robbins and Barker, 1973); however, both pearl millet hybrids tested in this study were relatively poor hosts compared to cotton and corn. Furthermore, there were differences in reproduction between the two hybrids, with TifGrain 102 being more resistant than HGM-100 to this nematode. These results indicate that there are varying levels of resistance to *B. longicaudatus* among pearl millet hybrids.

Paratrichodorus minor: Reproduction of *P. minor* on the different crops was not consistent between experiments (crop x experiment interaction, $P = 0.0002$); therefore, the results of the two experiments are presented separately. The main difference between the two experiments was in final numbers of *P. minor* on corn: in experiment 1 numbers were low; whereas in experiment 2 numbers were high relative to the other crops (Fig. 2). For the other crops, final nematode numbers were greatest ($P \leq 0.05$) on cotton and HGM-100, and least on peanut and TifGrain 102. In experiment 1, Rf values for *P. minor* on HGM-100, cotton, TifGrain 102, corn, and peanut were 103, 98, 34, 24, and 1, respectively. In experiment 2, Rf values on HGM-100, cotton, corn, TifGrain 102, and peanut were 304, 243, 239, 55 and 33, respectively.

The extremely high reproductive rates of *P. minor* on cotton, corn, and HGM-100 were somewhat surprising given that this nematode is typically not found in large numbers in soil from field crops (McSorley and Gallaher, 1991, 1993; Rodríguez-Kábana et al., 1993). Similarly, high reproductive rates were observed by Schilt and Cohn (1975) on cotton in a greenhouse study. Although the fecundity of *P. minor* is not known, the relatively short life cycle (16 to 17 days at 30 °C) may, in part, explain its rapid increase in numbers (Rohde and Jenkins, 1957). Perhaps the low numbers found in the field are due to insufficient moisture in the top 20 cm of soil. Trichodorid nematodes are susceptible to desiccation, and their numbers in upper layers of soil are often correlated with rainfall or irrigation (Cooke and Draycott, 1971; Decreamer, 1995; Mojtahedi and Santo, 1999; Wyss, 1970). Rapid increase in numbers of *P. minor* has been reported following soil fumigation and solarization (McSorley and McGovern, 2000; Perry, 1953). Such rapid increase may also occur following periods of extended rainfall (Cooke and Draycott, 1971).

Our results confirm that corn and cotton are good hosts for *P. minor* (Ayala et al., 1970; Brodie et al., 1970a; McSorley and Gallaher, 1991; Rohde and Jenkins, 1957; Schilt and Cohn, 1975). Peanut has been reported to be a poor or nonhost for *P. minor* (Baujard and Martiny, 1995). In our study, peanut was a poor host relative to corn and cotton; however, in experi-

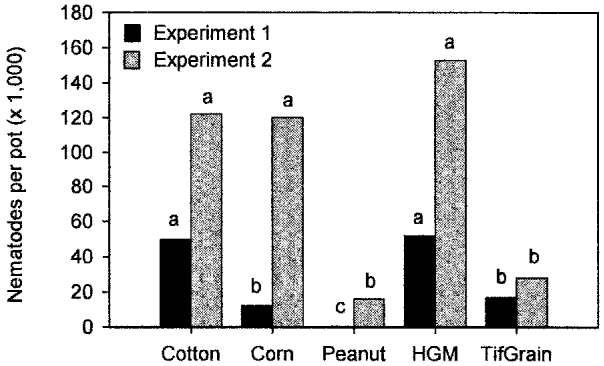

FIG. 2. Reproduction of *Paratrichodorus minor* on cotton (*Gossypium hirsutum*), corn (*Zea mays*), peanut (*Arachis hypogaea*), and two pearl millet (*Pennisetum glaucum*) hybrids, HGM-100 and TifGrain 102. Bars are the mean of nine (experiment 1) and eight (experiment 2) replicates. Within an experiment, bars with the same letter are not different ($P > 0.05$) based on Fisher's LSD test.

ment 2, the Rf on peanut was 33, which would be considered an excellent host in other nematode/host associations. For all the crops, reproduction of *P. minor* was greater in experiment 2 than in experiment 1, suggesting that environmental conditions were more conducive to survival and reproduction of the nematode in the second experiment. We conclude that, under optimal conditions, significant reproduction of *P. minor* may occur on peanut.

Reproduction of *P. minor* was 3 to 5.5 times greater ($P \leq 0.05$) on HGM-100 than on TifGrain 102. In terms of host status, HGM-100 was equivalent to cotton, whereas TifGrain 102 was equivalent to peanut. This confirms our previous finding from a field study indicating that pearl millet hybrids vary in their level of resistance to *P. minor* (Timper et al., 2002). In that study, more *Paratrichodorus* sp. were found in plots with HGM-100 than in plots where hybrids had 117 (= Tift 454 inbred) as the male pollinator. This same pollinator is the source of resistance to *M. incognita* and *M. arenaria* in TifGrain 102.

Pratylenchus brachyurus: Reproduction of *P. brachyurus* on the different crops was not consistent between the experiments (crop x experiment interaction, $P = 0.01$); therefore, the results of the two experiments are presented separately. In both experiments, nematode numbers were greatest ($P \leq 0.05$) on cotton, intermediate on corn and peanut, and lowest on HGM-100 and TifGrain 102 (Fig. 3). Overall, reproduction of *P. brachyurus* was low on all crops. The highest Rf values occurred on cotton (2.4), corn (1.5), and peanut (1.5) in experiment 1. In experiment 2, Rf values were <1 for all crops except corn (Rf = 1.8).

The reason for the apparent low reproductive rate of *P. brachyurus* in this study is unknown. Perhaps reproduction was greater than measured, but most of the nematodes remained in the roots even after 7 days in the mist chamber. Hussey and Roncadori (1978) found that only 40% of *P. brachyurus* egressed from cotton roots after 7 days in a mist chamber. They suggested that longer periods of incubation are needed to extract young juveniles and eggs that were present when the roots were removed from soil.

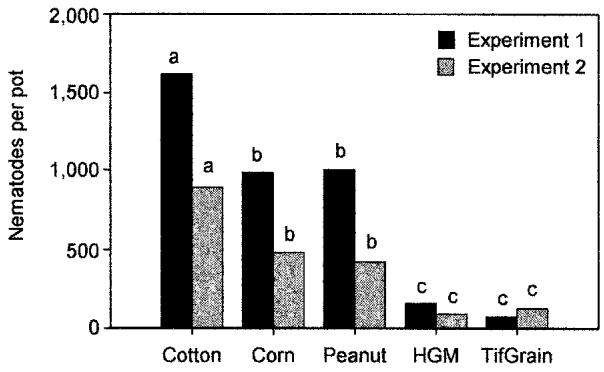

FIG. 3. Reproduction of *Pratylenchus brachyurus* on cotton (*Gossypium hirsutum*), corn (*Zea mays*), peanut (*Arachis hypogaea*), and two pearl millet (*Pennisetum glaucum*) hybrids, HGM-100 and TifGrain 102. Nematodes were extracted from both roots and soil. Bars are the mean of seven (experiment 1) and six (experiment 2) replicates. Within an experiment, bars with the same letter are not different ($P > 0.05$) based on Fisher's LSD test.

Several greenhouse and field studies found that corn and cotton were good hosts for *P. brachyurus* (Brodie et al., 1970b; Endo, 1959; Hussey and Roncadori, 1978; Jordaan et al., 1989; Machado and Inomoto, 2001; Payan and Dickson, 1988); however, reports on the host status of peanut have been inconsistent. Peanut was found to be a poor host (Rf < 1) for *P. brachyurus* by both Endo (1959) and Payan and Dickson (1988). In our study, reproduction of the nematode on peanut was similar to reproduction on corn. Likewise, Good et al. (1958) found equal numbers of *P. brachyurus* in the roots of peanut and sweet corn after 9 weeks' incubation in infested soil. Differences in nematode population or peanut cultivar could account for these conflicting reports, though no pathotypes of *P. brachyurus* have been reported and no commercial cultivars are known to have resistance to the nematode (Payan and Dickson, 1988; Starr, 1984).

Relative to cotton, corn, and peanut, both pearl millet hybrids were poor hosts for *P. brachyurus*. The reproductive rate of the nematode in our study was relatively low, even on good hosts such as cotton and corn, and it is possible that under some conditions, populations of *P. brachyurus* can increase on HGM-100 and TifGrain 102. Beaujard et al. (1995) reported an Rf > 1 for this nematode on pearl millet. A mixed population of *P. brachyurus* and *P. zeae* also increased on several different forage varieties of pearl millet in a field study (Johnson and Burton, 1973). In that study, the hybrids differed in their host status, with 'Tiflate' appearing to be more resistant to reproduction of the *Pratylenchus* spp. than the other hybrids. The two grain millet hybrids in our study were similar in their host status to *P. brachyurus*.

Meloidogyne javanica: Reproduction of *M. javanica* race 3 on the different crops was consistent between experiments; therefore, the combined data are presented. Nematode numbers were greatest ($P \leq 0.05$) on peanut, intermediate on corn and the two pearl millet hybrids, and lowest on cotton (Fig. 4). HGM-100 was a better ($P \leq 0.05$) host for *M. javanica* than TifGrain 102. A *t*-test was performed to determine whether HGM-100 and TifGrain 102 differed in the size of their root system which may, in turn, influence final nematode numbers. However, fresh root weight did not differ between the two hybrids ($P = 0.40$, $N = 29$). Reproductive factors for *M. javanica* on peanut, HGM-100, corn, and TifGrain 102 were 43, 6, 3, and 2, respectively. Cotton was a nonhost (Rf = 0.01) for *M. javanica*.

Three host races for *M. javanica* have been proposed: Race 1 does not reproduce on pepper or peanut, race 2 reproduces on pepper but not peanut, and race 3

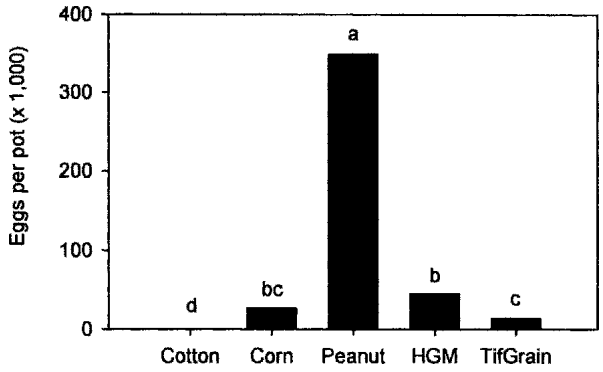

FIG. 4. Reproduction of *Meloidogyne javanica* race 3 on cotton (*Gossypium hirsutum*), corn (*Zea mays*), peanut (*Arachis hypogaea*), and two pearl millet (*Pennisetum glaucum*) hybrids, HGM-100 and TifGrain 102. Bars are the mean of 16 replicates from two experiments, and those with the same letter are not different ($P > 0.05$) based on Fisher's LSD test.

reproduces on peanut but not pepper (Sharma et al., 1995). Cotton is a nonhost for all three races (Hartman and Sasser, 1985). As expected, peanut was a good host and cotton a nonhost for the culture of *M. javanica* race 3 used in this study. Most corn hybrids are good hosts for *M. javanica,* with Rf values ranging between 2 and 16 (Ibrahim et al., 1991; Windham and Williams, 1988); our results also were within this range.

The host status of the two pearl millet hybrids for *M. javanica* was similar to corn. HGM-100 was more ($P \leq 0.05$) susceptible than TifGrain 102 to reproduction of the nematode. Similarly, HGM-100 also was more susceptible to *M. incognita* race 3 and *M. arenaria* race 1 than hybrids with either 114 or 117 (= Tift 454 inbred) as the male pollinator (Timper et al., 2002). Johnson et al. (1977) also reported resistance of some pearl millet cultivars to *Meloidogyne* spp., with 'Gahi 3' and Tiflate expressing resistance to all three species tested (*M. incognita, M. javanica,* and *M. arenaria*).

Of the two grain hybrids evaluated in this study, only TifGrain 102 is commercially available; HGM-100 is no longer available because it is susceptible to the rust fungus *Puccinia substriata* var *indica* (Wilson, pers. comm.). Our results demonstrated that TifGrain 102 was a poor host for *B. longicaudatus* and *P. brachyurus* (Rf < 1) and, relative to other crops tested, would be less likely to increase densities of *P. minor* and *M. javanica.* Therefore, this pearl millet hybrid should be a compatible rotation crop for cotton, corn, and peanut in fields infested with these nematodes. Pearl millet hybrids differ in the level of resistance to *B. longicaudatus, P. minor,* and *Meloidogyne* spp. (Johnson et al., 1977; Timper et al., 2002), and resistance to these nematodes should be incorporated into future hybrids.

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