

INTERACTIONS OF *HELICOTYLENCHUS DIHYSTERA*, *PRATYLENCHUS PSEUDOPRATENSIS*, AND *TYLENCHORHYNCHUS GLADIOLATUS* ON TWO PLANTS FROM THE SOUDANO-SAHELIAN ZONE OF WEST AFRICA

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ABSTRACT

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Interactions between *Helicotylenchus dihyстера*, *Pratylenchus pseudopratensis*, and *Tylenchorhynchus gladiolatus* were studied on millet (*Pennisetum typhoides*) and acacia (*Acacia holosericea*). Interactions between *H. dihyстера* and *P. pseudopratensis* were similar on both plants; reproduction of each was lower when the other nematode species was present. *T. gladiolatus* reproduction was stimulated in the presence of the other species on millet, whereas it was inhibited on acacia at the lowest inoculum levels (50 and 200 nematodes/plant). Damage to plants was not density dependent. Damage to millet differed with the species composition of the community. Only monospecific populations of *T. gladiolatus* and *P. pseudopratensis* significantly reduced the millet biomass, particularly the root system. *H. dihyстера* reduced the pathogenicity of the two other species on this plant. Each nematode assemblage suppressed dry shoot and root weight of acacia; most assemblages reduced the number of *Rhizobium* nodules on the root system.

Key words: *Acacia holosericea*, competition, *Helicotylenchus dihyстера*, nematode interactions, *Pennisetum typhoides*, *Pratylenchus pseudopratensis*, *Tylenchorhynchus gladiolatus*.

RESUMEN

Villenave, C. y P. Cadet. 1998. Interacciones entre *Helicotylenchus dihyстера*, *Pratylenchus pseudopratensis*, y *Tylenchorhynchus gladiolatus* en dos plantas de la zona Soudano-Saheliana del oeste de Africa. *Nematropica* 28:31-39.

Se estudiaron interacciones entre *Helicotylenchus dihyстера*, *Pratylenchus pseudopratensis*, y *Tylenchorhynchus gladiolatus* en mijo (*Pennisetum typhoides*) y acacia (*Acacia holosericea*). Las interacciones entre *H. dihyстера* y *P. pseudopratensis* fueron similares en ambas plantas; la reproducción de cada uno fue menor, cuando el otro estuvo presente. La reproducción de *T. gladiolatus* fue estimulada en presencia de las otras especies en mijo, mientras que fue inhibida en acacia, a los niveles de inóculo menores (50 y 200 nematodos por planta). El daño a las plantas fue independiente de la densidad. El daño del mijo fue diferente, dependiendo de la composición de especies de la comunidad. Solamente poblaciones mono-específicas de *T. gladiolatus* o *P. pseudopratensis* redujeron significativamente la biomasa del mijo, particularmente del sistema de raíces. *H. dihyстера* redujo la patogenicidad de las otras dos especies en esta planta. Todos los ensamblamientos de nematodos, suprimieron el peso seco de las ramas y raíces en acacia. La mayoría de estos ensamblamientos, redujeron el número de nódulos de *Rhizobium* en el sistema de raíces.

Palabras claves: *Acacia holosericea*, competencia, *Helicotylenchus dihyстера*, interacciones entre nematodos, *Pennisetum typhoides*, *Pratylenchus pseudopratensis*, *Tylenchorhynchus gladiolatus*.

INTRODUCTION

The cropping system in peanut-growing areas of Senegal is based on peanut-millet rotation alternating with short fallow periods. As in most tropical and subtropical ecosystems, communities of plant parasitic nematodes consist of numerous species (Baujard *et al.*, 1989; Luc *et al.*, 1990). The most abundant species are *Scutellonema cavenessi* Sher, 1964, *Helicotylenchus dihystrera* Cobb, 1893, *Tylenchorhynchus gladiolatus* Fortuner and Amougou, 1973 and *Pratylenchus pseudopratensis* Seinhorst, 1968. The use of different nematocides in field studies was effective for nematode control and increased the yield of both millet and peanut. The effects on crop yields may have resulted from both a decrease in soil nematode populations and direct phytostimulation (Baujard, 1994). When studied individually on millet, *H. dihystrera* and *T. gladiolatus* were found to be pathogenic, whereas *S. cavenessi* was not (Baujard and Martiny, 1995a; Baujard and Martiny, 1995b; Villenave *et al.*, 1997).

Population dynamics and pathogenicity of concomitant populations of plant-parasitic nematodes may differ from those when the populations occur individually. Species of plant-parasitic nematodes may interact ecologically as competitors and etiologically in their effect on plant growth and crop production (Eisenback and Griffin, 1987). Phytoparasitic nematodes must compete when their niches overlap and when substrate availability is limited (Norton, 1989). Depending on the species comprising a community, the negative effect on plant growth of pathogenic phytoparasitic nematode species may be increased (Sikora *et al.*, 1972) or decreased (Duncan and Ferris, 1983; Estores and Chen, 1970).

The aim of this study was to determine the nature of the interactions between *H.*

dihystrera, *P. pseudopratensis*, and *T. gladiolatus*, and to determine the effect of concomitant populations of these nematodes on growth of millet (*Pennisetum typhoides*, (L.) Rich.) and acacia (*Acacia holosericea*, A. cunn. ex G. Don.) in microcosm experiments. The plants were chosen for study because millet is the major food crop in the region and acacia has considerable potential for use in reforestation in Sahelian areas, and may grow adjacent to millet-peanut fields.

MATERIALS AND METHODS

Inoculum: Populations of *Pratylenchus pseudopratensis*, *Helicotylenchus dihystrera*, and *Tylenchorhynchus gladiolatus* were maintained on millet (cv. IKMV-8201) in a greenhouse. Inoculum of *P. pseudopratensis* was obtained by plugging infected roots in a mist chamber (Seinhorst, 1950), and inocula of *H. dihystrera* and *T. gladiolatus* were extracted from soil using a Seinhorst elutriator (Seinhorst, 1962).

Interaction on millet: PVC plastic tubes (4.5 cm diam., 17.5 cm long) were filled with autoclaved soil (40 minutes at ca. 140°C) and placed in a constant-temperature wooden box at 29 ± 2°C in a greenhouse. The soil (sand 83.8%, silt 8%, clay 8.2%, carbon content 3.1%, pH H₂O 5.5, cation exchange capacity 2.72 meq.%) was collected from a millet field near Bambey (15°20'N, 17°30'W), Senegal.

Millet seeds were germinated in tap water for 3 days and one seedling was transplanted into each tube. Nematode inoculation was carried out 5 days after the millet transplantation. The nematodes were poured into a hole (5 mm by 10 mm) to one side of the seedling and covered with soil. The plants were watered daily with tap water.

Nematodes combinations compared were: 1) H = *H. dihystrera*; 2) P = *P. pseudopratensis*; 3) T = *T. gladiolatus*; 4) HP

= *H. dihystra* + *P. pseudopratensis*; 5) PT = *P. pseudopratensis* + *T. gladiolatus*; 6) HT = *H. dihystra* + *T. gladiolatus*; 7) HPT = *P. pseudopratensis* + *H. dihystra* + *T. gladiolatus*. Inoculum levels (Pi) were 50, 200, and 600 nematodes per pot for each species, to give 0.2, 0.8, and 2.4 nematodes per cm³ of soil which are similar to densities found in the field (Cadet and Floret, 1995). The 21 treatments (50H, 50T, 50P, 50H + 50T, 50H + 50P, 50T + 50P, 50H + 50T + 50P, 200H, 200T, 200P, 200H + 200T, 200H + 200P, 200T + 200P, 200H + 200T + 200P, 600H, 600T, 600P, 600H + 600T, 600H + 600P, 600T + 600P, 600H + 600T + 600P) were replicated 10 times. The growth of inoculated plants was compared to that of non-inoculated controls, replicated 30 times.

The nematodes were extracted from the soil and roots (mist chambers) 65 days after inoculation (Seinhorst, 1950, 1962). The roots from all the treatments (even nematode-free control) were placed in mist chambers before drying. Final populations (Pf) were determined by summing total nematodes from the soil and roots and the reproduction rate (Pf/Pi) per tube was calculated. The roots and shoots were dried for 4 days at 70°C before weighing.

Final nematode numbers were transformed by $\log(x+1)$ prior to one-way analysis of variance. The effect of the size of inoculum on the plant biomass was ana-

lyzed for each host-nematode combination by regression. Two-way anova and one-way anova were performed for the vegetative biomass; means were compared with L.S.D. and differences noted in the discussion were significant at $P=0.05$.

Interaction on acacia: acacia seeds were treated with concentrated sulphuric acid for 30 minutes. They were washed for 12 h in sterile distilled water and planted in polyethylene bags filled with autoclaved soil. After one month, each seedling was transplanted into a PVC-tube. Nematodes were inoculated 10 days later. Soil temperature, nematode treatments, data analyses, and all experimental procedures were as described for millet. Treatments were replicated seven times (except nematode-free controls, with 21 replicates). Nematodes in each treatment were extracted 70 days after inoculation. Both the roots and shoots were dried and weighed. Root nodules were counted; the soil was contaminated by indigenous *Rhizobium* coming from tap water.

RESULTS

More than 90% of the *T. gladiolatus* and *H. dihystra* recorded were found in the soil on both plants, whereas *P. pseudopratensis* was found mainly in the roots (Table 1).

The final number of *H. dihystra* always increased on millet irrespective of the spe-

Table 1. Distribution of the final nematode populations between soil and roots (%) for the three nematode species on the two host plants.

	Soil		Roots	
	Millet	Acacia	Millet	Acacia
<i>Helicotylenchus dihystra</i>	96.3	95.1	3.7	4.9
<i>Pratylenchus pseudopratensis</i>	15.7	29.2	84.3	70.8
<i>Tylenchorhynchus gladiolatus</i>	99.8	99.8	0.2	0.2

cies composition of the community (Fig. 1-A). The reproductive rate of *H. dihystra* was higher on millet than on acacia; Pf/Pi ranged from 5.9 to 12.5 on millet and 1.3 and 2.3 on acacia when inoculated alone. *H. dihystra* was particularly inhibited by *T. gladiolatus* regardless of the inoculum dose, nematode combination, or host. The antagonistic effect of *T. gladiolatus* on *H. dihystra* was higher on acacia than on millet. At the highest inoculum level, *T. gladiolatus* reduced the final number of *H. dihystra* 10 and 13 times, respectively, with and without *P. pseudopratensis*. The antagonistic effect of *P. pseudopratensis* alone to *H. dihystra* was only significant on acacia when the inoculum dose was 200 individuals.

The final numbers of *T. gladiolatus* decreased on the two plants as the inoculum increased, in most treatment combinations, except with *P. pseudopratensis* (TP) (Fig. 1-B). The nematode reproduced better on millet than on acacia. The minimum reproduction rate of *T. gladiolatus* was 5.8 as a single species on millet and 0.8 on acacia when inoculated with *H. dihystra* and *P. pseudopratensis*. At the lowest densities, *H. dihystra* stimulated the reproduction of *T. gladiolatus* on millet, whereas it had a negative effect on acacia. The same trend was observed when *T. gladiolatus* was inoculated with *H. dihystra* and *P. pseudopratensis* together, but the effects were less evident. On both plants, the presence of *P. pseudopratensis* favored the multiplication of *T. gladiolatus* at the highest density (600). This effect was not seen when both *P. pseudopratensis* and *H. dihystra* were present.

The reproduction rate of *P. pseudopratensis* on millet ranged from 2.8 to 7.2 when it was inoculated alone (Fig. 1-C). In contrast, *P. pseudopratensis* failed to increase on acacia (reproduction rate between 0.13 and 0.96 when it was inoculated alone).

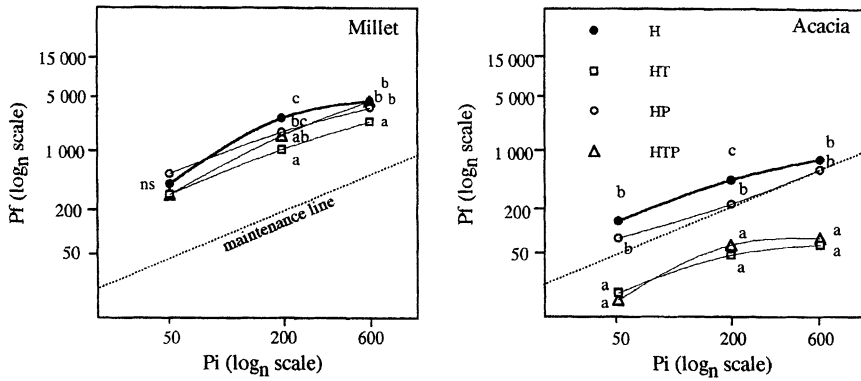
However, Pf/Pi was inversely related to Pi, suggesting that intraspecific competition existed and that acacia is a host, albeit poor, for this species. Interactions between *P. pseudopratensis* and the two other species were comparable on both millet and acacia. The final numbers of *P. pseudopratensis* were lower on the two plants when *T. gladiolatus* was also inoculated, either alone or together with *H. dihystra* (except on millet at the medium density). The presence of *H. dihystra* had no effect on the final number of *P. pseudopratensis* on the two plants (except on millet at medium inoculum).

Pathogenicity: The nematode effect on the shoot and root dry weights of both host plants was significant, but the inoculum level had no significant effect according to anova (Table 2). Neither was acacia biomass (roots and aerial parts) significantly related to the nematode inoculum level, according to linear regression, regardless of the nematode treatment (Table 3). In only 5 cases were significant relationships measured on millet between level of inoculum and plant biomass: root biomass for HP and shoot biomass for HT and HTP (negative slopes); and root biomass and total biomass for P (positive slopes).

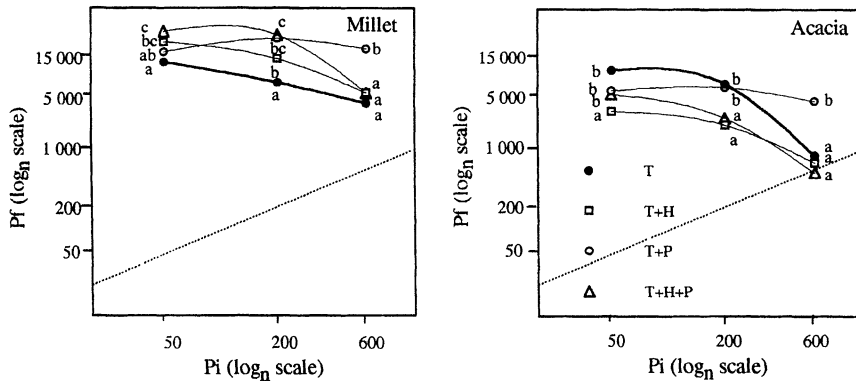
The different nematode assemblages did not cause a significant reduction in the shoot biomass of millet when compared to the control, except for plants inoculated with *H. dihystra* plus *T. gladiolatus* which show a 12% increase (Table 3-A). Root biomass was significantly lower in the presence of T, P, TP, HT when compared to the control. In three treatments out of four with *H. dihystra* the root biomass was not lower than in the noninoculated control.

The total millet biomass was significantly reduced only in treatments T (-13%) and P (-9%); however, biomass was not reduced when T and P were inoculated together. *H. dihystra* was the only species that did not cause significant damage to

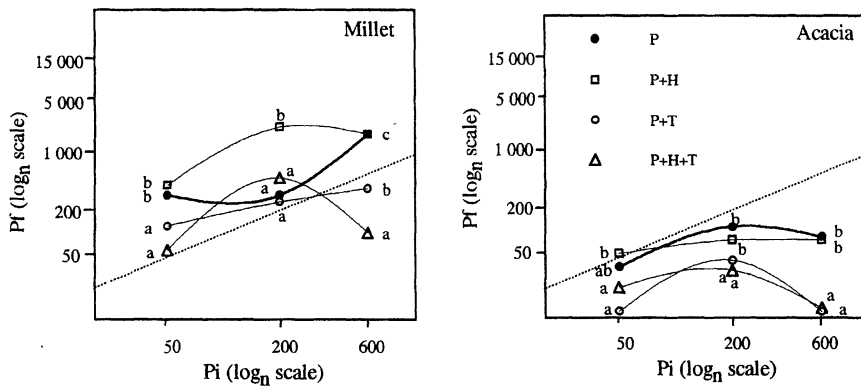
A- *Helicotylenchus dihystera*



B- *Tylenchorhynchus gladiolatus*



C- *Pratylenchus pseudopratensis*



1. Relationships between inoculum size (Pi) and final nematode numbers (Pf) in nematode communities variably comprised of *Helicotylenchus dihystera* (H), *Tylenchorhynchus gladiolatus* (T), *Pratylenchus pseudopratensis* (P). Each Pi, data marked with different letters are significantly different ($P < 0.05$)

Table 2. Results of two-way ANOVA on the effects of nematode treatments and inoculum dosages on plant biomass.

	Millet		Acacia	
	Shoots	Roots	Shoots	Roots
Nematode treatments (N)	*	***	*	***
Inoculum levels (IL)	n.s.	n.s.	n.s.	n.s.
N × IL	*	**	*	**

^zp < 0.001 ***, p < 0.01 **, p < 0.05 *, n.s. = not significant.

millet roots when inoculated alone. None of the nematode combination treatments were detrimental to total millet biomass.

The shoot biomass of all infested acacia plants was reduced, compared to the non-inoculated plants, irrespective of the nematode community composition (Table 3-B). Likewise, compared with the control, the root biomass was significantly lower with most of the nematode assemblages (except H and T). The reduction in total biomass ranged from 12 to 20% for all the nematode assemblages. *H. dihystra* inoculated alone was the only nematode treatment that did not reduce total acacia biomass, although *H. dihystra* together with other nematode species damaged *A. holosericea*. All nematode combinations except *H. dihystra* and *P. pseudopratensis* inhibited nodulation on *A. holosericea* roots.

DISCUSSION

There was strong intraspecific competition among *T. gladiolatus*. For all treatments (except TP) the final population density of *T. gladiolatus* decreased when the inoculum level increased on the two plants. The same trend was observed with *P. pseudopratensis* on the two plants when the inoculum was in the range 200-600 nematodes. This intraspecific competition may be the result of the young age of the plants at the inoculation date.

Millet is a good host for the three nematode species. However, *A. holosericea* is a good host for *T. gladiolatus* and *H. dihystra* only, since fewer *P. pseudopratensis* than inoculated were recovered on *A. holosericea*.

Different kinds of interactions were observed between the three nematode species studied: 1) competition—interactions detrimental to both species (T(-) and H(-) on acacia); 2) amensalism—neutral for one species and detrimental for the other (T(0) and P(-) on acacia); 3) antagonism—beneficial for one species and detrimental to the other (T(+)) and H(-) on millet; T(+) and P(-) on millet); and 4) neutralism—the simultaneous presence of *H. dihystra* and *P. pseudopratensis* had little effect on the reproduction of either species. Most of the interactions were detrimental to at least one species, primarily for *P. pseudopratensis* or *H. dihystra* when *T. gladiolatus* was present. Adverse interactions between nematodes can occur when one of the species reduces the number of feeding sites (preemptive competition), changes the physiology of the host to alter its suitability (chemical competition), or reduces the quantity of available food resources (consumptive competition) (Umesh *et al.* 1994). These different mechanisms for competition are not mutually exclusive and the present study does not discriminate among them. However, inter-

Table 3. Effect of the different nematode treatments^w on millet and acacia biomass (g dry weight plant⁻¹).

A- Millet								
	H [*]	T	P	TP	HT	HP	HTP	C
Shoots	1.36 (abc) ^y	1.25 (a)	1.29 (ab)	1.40 (bc)	1.46 ^z (c)	1.35 (abc)	1.38 ^z (abc)	1.3 (ab)
Roots	0.56 (cde)	0.42 (a)	0.46 ^z (ab)	0.53 (bcd)	0.49 (abc)	0.68 ^z (f)	0.59 (de)	0.62 (ef)
Total	1.92 (b)	1.67 (a)	1.75 ^z (a)	1.93 (b)	1.95 (b)	2.03 (b)	1.97 ^z (b)	1.92 (b)
B- Acacia								
	H	T	P	TP	HT	HP	HTP	C
Shoots	0.52 (a)	0.53 (a)	0.49 (a)	0.56 (a)	0.50 (a)	0.52 (a)	0.48 (a)	0.62 (b)
Roots	0.41 (b)	0.34 (ab)	0.3 (a)	0.32 (a)	0.30 (a)	0.29 (a)	0.31 (a)	0.39 (b)
Total	0.93 (ab)	0.87 (a)	0.79 (a)	0.88 (a)	0.80 (a)	0.81 (a)	0.79 (a)	1.01 (b)
number of nodules per plant	2.3 (bc)	0.7 (a)	2.6 (bc)	1.4 (ab)	0.2 (a)	0.5 (a)	0.6 (a)	2.9 (c)

^wPi for each treatment pooled for analysis.

^{*}*Helicotylenchus dihystrera* (H), *Tylenchorhynchus gladiolatus* (T), *Pratylenchus pseudopratensis* (P), uninoculated control (C).

^ydata followed by different letters in the same line are significantly different ($P < 0.05$).

^zsignificant ($P < 0.05$) negative regression slope between plant biomasses and level of nematode inoculation.

^zsignificant ($P < 0.05$) positive regression slope between plant biomasses and level of nematode inoculation.

actions beneficial to *T. gladiolatus* when combined with other species on millet may have resulted from a mechanical or a physiological alteration of the plant causing millet to become a more suitable host. Physiological changes induced by plant parasitic nematodes may also enhance nutrition or reduce the host resistance to the parasite (Eisenback and Griffin, 1987).

Two of the species used in our experiments, *T. gladiolatus* and *H. dihystrera* are ectoparasites whereas *P. pseudopratensis* is a

migratory endoparasite. The nature of parasitism greatly influences the degree of interaction between species (Eisenback, 1993). Although competition is generally more severe between species with similar feeding habits, and competitive advantage seems to increase as the host-parasite relationship becomes more complex, this was not apparent in the conditions of the experiment.

Only one interaction among these two species was density-dependent. *P. pseudopratensis* on millet and acacia inhibited the mul-

tiplication of *T. gladiolatus* at the low inoculum dose (50) whereas at the high inoculum dose (600), the nematode favored the multiplication of *T. gladiolatus*. The interactions between species may be affected by host suitability. The presence of the other nematodes reduced reproduction of *T. gladiolatus* on acacia whereas the reproduction of *T. gladiolatus* was stimulated by other species on millet. While *H. dihystra* population densities on both plants were suppressed by the presence of *T. gladiolatus*, the effect were greater on acacia.

Most experimental studies on the pathogenicity of nematodes only consider the effects of a single species. However, in tropical conditions, communities of plant parasitic nematodes consist of numerous species each of which may modify the pathogenicity of the others. When the amount of disease caused by several nematode species is proportional to the effect of each alone, there is no interaction. Negative interaction occurs when the amount of disease caused by several nematode species is less than the effect of each alone, and positive (or synergistic) interaction is the opposite. Most of the positive interactions that have been reported involved a species of *Meloidogyne* and some other endoparasite (Eisenback, 1993).

Only monospecific populations of *T. gladiolatus* and *P. pseudopratensis* significantly reduced the biomass of millet by 13% and 9%, respectively. *H. dihystra*, which had no pathogenic effect on millet, has been reported to be a weak pathogen on several hosts (Birchfield, 1984; Spaul and Cadet, 1990).

The degree of plant damage was affected by interactions between the species of plantparasitic nematodes. These interactions limited plant injury to lower values than those observed with each species alone. Similar results were reported by Estores and Chen (1970) and Umesh and Ferris (1994) with different species of

Meloidogyne and *Pratylenchus*. In our experiments, it seems that competition with the less virulent species, *H. dihystra*, reduced the virulence of the two other species, a type of interaction reported previously (Duncan and Ferris, 1983). Equally likely is that *H. dihystra* caused physiological changes in the plant, since its presence did not greatly affect reproduction of the other species.

All nematode assemblages significantly reduced the plant biomass of *A. holosericea* except *H. dihystra*. However, no differences in the level of pathogenicity occurred between the different nematode treatments based on the total plant biomass (except for H). Neither were there any interactions between nematode species on the growth of acacia. The significant reduction in the number of nodules on this leguminous plant, observed with most of the nematode assemblages, may result in lower nitrogen fixation and reduced biomass accumulation in the roots and aerial parts. A similar result on acacia was observed with *Meloidogyne javanica* (Duponnois *et al.*, 1995).

The use of nematicides to manage nematodes is no longer an economic solution in developing countries, like Senegal. Knowledge of interactions between nematodes species could lead to new ways of manipulating the structure of phytoparasitic nematode communities in order to limit their pathogenicity. For example, *H. dihystra* seemed to reduce the damage caused to millet by the other species. Methods to favor selected species, antagonistic to pathogenic species, may include mesological relationships (Cadet *et al.*, 1997) or rotations with hosts favorable to antagonists, particularly following fallow periods (Cadet and Floret, 1995).

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