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Effect of plant parasitic nematodes on the sustainability of a natural fallow cultural system in the Sudano-Sahelian area in Senegal

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Abstract – To study the influence of fallow on plant parasitic nematodes and soil fertility, the difference in the growth of millet in a greenhouse was compared in sterilized and naturally infested soil. These soils are ferruginous and were taken from a 17-year-old fallow plot and a neighbouring cultivated field, located in the region of Thysse Kaymor in Senegal. The plant-parasitic nematode community of the previously cultivated soil consisted primarily of two species: an ectoparasite, *Tylenchorhynchus gladiolatus*, and an endoparasite, *Scutellonema cavenessi*. The soil from the fallow plot was infested with many species, but under the influence of the millet crop, it evolved towards the two species situation observed in the cultivated soil, except that under the experimental conditions (in pots), *Pratylenchus pseudopratensis* replaced *S. cavenessi*. Whether or not the soil was infested with nematodes, the previous fallow period had a positive effect on the development of successive millet crops. The impoverishment of the soil through repeated cultivation and the impact of nematodes both reduced crop growth. The two factors evolved in the same way, that is a decrease in the development rate of the millet as the number of crop cycles increased. The symptoms of soil impoverishment can be corrected, either by suppressing the nematodes or by fallowing. © 2000 Éditions scientifiques et médicales Elsevier SAS

Sudano-Sahelien area / plant parasitic nematodes / sustainability / fallow / millet

Résumé – Influence des nématodes phytoparasites sur la durabilité d'un système de culture à jachère naturelle dans la zone soudano-sahélienne du Sénégal. Afin d'étudier l'influence de la jachère sur les nématodes phytoparasites et la fertilité du sol, la croissance du mil en serre a été comparée dans des sols stérilisés et naturellement infestés de la région de Thyssé-Kaymor au Sénégal. Ces sols sont ferrugineux et ont été collectés dans des parcelles voisines, l'une en jachère depuis 17 ans et l'autre cultivée depuis plusieurs années. Le peuplement de nématodes du sol cultivé est constitué principalement de deux espèces : un ectoparasite, *Tylenchorhynchus gladiolatus*, et un endoparasite, *Scutellonema cavenessi*. Le sol de la jachère est infesté par de nombreuses espèces, mais sous l'influence de la culture de mil, il évolue vers la situation simplifiée observée dans les sols cultivés, exception faite que dans nos conditions expérimentales, en pots, *Pratylenchus pseudopratensis* remplace *S. cavenessi*. Que le sol soit ou non infesté de nématodes, la jachère précédente a un effet positif sur le développement du mil à chaque cycle. L'appauvrissement du sol, comme l'impact des nématodes, réduisent la croissance du mil. Les deux facteurs évoluent dans le même sens, c'est-à-dire une diminution du développement du mil au fur et à mesure que le nombre de cycles culturaux augmente. Les symptômes d'épuisement du sol peuvent êtres rectifiés, soit en supprimant les nématodes, soit en pratiquant la jachère. © 2000 Éditions scientifiques et médicales Elsevier SAS

Zone soudano-sahélienne / nématodes phytoparasites / durabilité / jachère / mil

1. INTRODUCTION

Fallowing, by abandoning land to natural vegetation, is an ancient practice used when crop yields fall and when there are no other means of compensating for the drop in fertility. However, fallowing is a restraining factor for the farmers who, whatever their technical level, would prefer to continue cultivation. The disap-

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pearance of fallow is generally a necessity resulting from the increasing demands for land of a growing human population [14]. However, permanent cultivation of land without significant inputs leads to a 'mining' of nutrients. The soil becomes impoverished by repeated cropping without compensation by fertilizers [24]. It is, therefore, necessary to decide whether or not fallow, despite its limitations, is a worthwhile practice.

During the fallow period, the growth of plants and other living organisms produce an accumulation of mineral elements and organic matter which become available to the crop when the ground is cleared for cultivation [9, 12]. Together with these beneficial organisms, plant parasites, such as nematodes, also develop. Like other plant pathogens, nematodes are likely to reduce crop yields [15]. In the Sudano-Sahelien region of Senegal, they are abundant on cultivated plants [11]. Recent studies have shown that fallowing reduces the abundance of the nematode species parasitizing food crops, but increases species diversity and overall abundance of the phytoparasitic nematode trophic group [6, 16, 22].

To evaluate sustained benefits of fallow and the impact of nematode communities, it is normally necessary to make in situ observations over several years. However in this study, the time scale was reduced by the combination of two techniques: i) using soil from old fallow land and from land that had been cultivated for many years; and ii) working in a glasshouse which allowed several cropping cycles over a short period of time. The aim of this work was to determine the impact of natural fallow and of plant parasitic nematodes on the performance of millet in microcosm experiments.

2. MATERIALS AND METHODS

Soil was collected at a depth of 3–15 cm from a tropical, ferruginous soil [8] from a 17-year-old natural fallow land, hereafter referred to as fallow soil, and from a near-by millet field cultivated for more than 20 years. These plots were situated in the Thysse Kaymor region of Senegal that receives about 700 mm of rainfall per year.

In the laboratory, part of the soil from each site was sterilized by autoclaving (130 °C, 2 h). The sterilized and the naturally infested soils were then added to 2.5-L pots in which a pre-germinated millet seed (variety IKMV-8201) was planted. The number of replicates per treatment ranged from 9 to 11. Each pot was watered daily with 100–200 cm^3 of distilled water, depending on the age of the plants. After 2 months, the millet was removed and the roots separated from the soil which was then put back in the pots for a new crop cycle.

Three successive cycles of millet, each of 2-month duration, were grown in the same soil from May to October over 2 years, giving a total of six cycles. This period corresponds to the hot, humid season during which crops are grown in Senegal.

Because the millet size decreased from one cycle to the next, the nutrient solution of Bouhot and Bonnel [4] was applied during the first week of growth at the beginning of the 4th and 6th cycles of the 2nd year (100 $cm^3 \cdot d$). During the period between the two growing seasons, the cold dry season from October to May, the pots were kept under glasshouse conditions without watering and without plants.

At the end of each cycle which lasted for 7 or 8 weeks, the height of the plants was measured and the roots and shoots were weighed. When sterilized and non-sterilized treatments were compared, the vegetative results of the 1st cycle were not included in the calculation of averages, because the plant growth was artificially stimulated by the release of plant nutrients following the sterilization process [1]. For each of the four soil conditions, sterile/non-sterile, fallow/cultivated, the averages of individual crop cycles or of crop cycles 2 to 6 combined, were compared two by two with the Student's t-test ($P > 0.05$) or with the Mann-Withney U-test, when the variances were significantly different (F-test; $P < 0.05$).

For nematode investigations, a small quantity of soil (less than 100 cm^3) was sampled from each pot and mixed per treatment, prior to processing. This composite soil sample method was used to avoid collecting too much soil from the pots. But this method eliminates the possibility of calculating the variability of the nematode data. Nematodes were separated from the composite soil and roots sample by the Seinhorst methods [18, 19]; they were then identified and counted.

3. RESULTS

3.1. Nematode communities

Fallow soil contained five common species of plant parasitic nematode: *Scutellonema cavenessi*, *Helicotylenchus dihystera*, *Tylenchorhynchus gladiolatus*, *T. mashoodi* and *Pratylenchus pseudopratensis*. Soil from cultivated land contained only two of these species: *S. cavenessi* and *T. gladiolatus*.

3.2. Evolution of nematode densities in soil and roots

At the end of each crop cycle, the soil nematode community of the previously cultivated soil was always larger than that of the previously fallowed soil, but the community developed in the same way, with a strong increase in numbers in the 1st and 5th cycles (*figure 1A*). The reverse situation was observed in the roots. There were generally more nematodes in the millet roots in the fallow soil than in the cultivated soil, in particular, in the 2nd, 4th and 5th crop cycles (*figure 1B*).

3.3. Changes in nematode species composition

The nematode infestation of the cultivated soil consisted primarily of two species *S. cavenessi* and *T. gladiolatus*. The proportion of *S. cavenessi* increased with each cycle until the 5th cycle (*figure 1C*).

In the fallow soil, the nematode species composition changed considerably with the millet crop cycles. Many species disappeared or appeared randomly (*figure 1C*). During the last cycle, both soils contained only two species in similar proportions: *T. gladiolatus* and *P. pseudopratensis* in the fallow soil; *T. gladiolatus* and *S. cavenessi* in the cultivated soil.

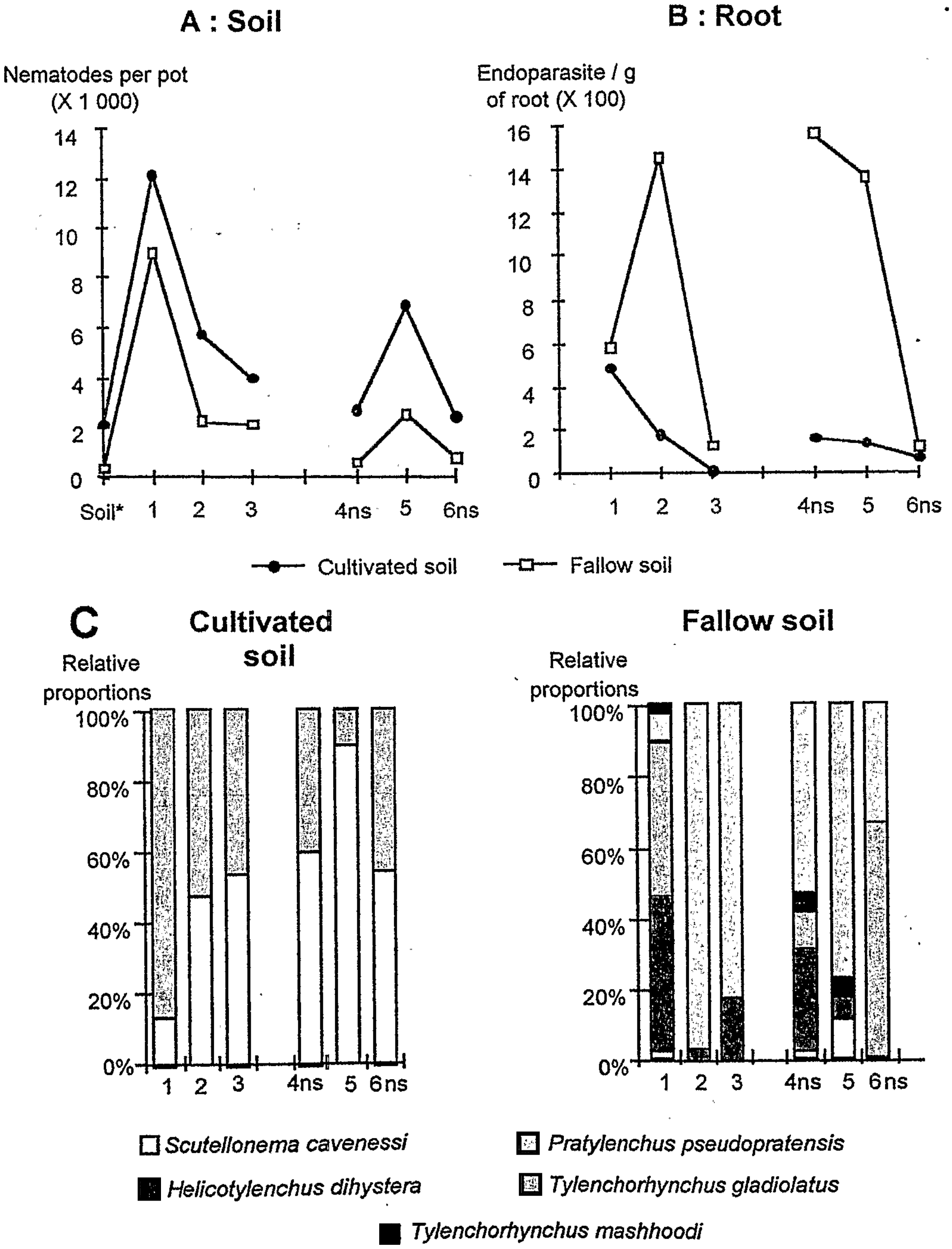

Figure 1. Changes in the number and species of plant parasitic nematode communities over the six crop cycles of 2 months in greenhouse pot experiments on millet (obtained from the single composit sample analysis at the end of each cycle). (A) Soil communities; (B) root populations; (C) nematode species present in the fallow and cultivated soils. Soil, Field and fallow infestation when soil was collected at the end of the dry season; ns, nutrient solution; 1 to 6, crop cycle.

Table I. Comparison of the millet characteristics (average of nine to eleven replicates per crop cycle): height (cm), shoot and root biomass (g), for the four situations – fallow or cultivated soil, infested or non-infested soil – and the averages of the crop cycles 2 to 6 combined. Numbers with the same letter are not statistically different ($P < 0.05$): Student's t-test or Mann-Withney U-test, when variances are statistically different (F-test; $P < 0.05$). Capital letter, horizontal comparison between cultivated and fallow infested soil. Greek letter, horizontal comparison between cultivated and fallow sterilized soil. Lower-case letter, horizontal comparison between infested and non-infested soil for each soil origin.

		Cultivated soil		Fallow soil	
		I	II	III	IV
		Infested	Sterilized	Infested	Sterilized
Height	Cycle 1	12.92 aA	71.46 bα	24.42 aB	86.36 bα
	Cycle 2	24.1 aA	19.51 aα	27.83 aA	20.3 aα
	Cycle 3	29.14 aA	20.53 aα	46.58 aB	38.58 aα
	Cycle 4	45.67 aA	67.17 aα	53.22 aA	77.72 aα
	Cycle 5	26.83 aA	75.08 bα	41.61 aA	98.1 bα
	Cycle 6	33.16 aA	35.66 aα	32.27 aA	34.72 aα
Crop cycles 2 to 6 combined	Average	31.5 aA	42.6 aα	40.5 aB	54.9 aα
Shoot biomass	Cycle 1	3.28 aA	49.14 bα	4.51 aB	53.54 bα
	Cycle 2	6.07 aA	7.5 aα	10.71 aB	12.08 aα
	Cycle 3	6.04 aA	8.34 bα	10.06 aB	14.32 aβ
	Cycle 4	19.87 aA	35.54 bα	26.43 aA	43.02 bβ
	Cycle 5	14.81 aA	35.68 bα	21.17 aA	30.98 bα
	Cycle 6	9 aA	11.74 bα	9.67 aA	9.5 aβ
Crop cycles 2 to 6 combined	Average	11.0 aA	19.3 bα	15.4 aB	22.7 bα
Root biomass	Cycle 1	2.05 aA	8.79 bα	1.86 aA	9.67 bα
	Cycle 2	1.53 aA	2.29 bα	2.21 aB	2.25 aα
	Cycle 3	1.46 aA	1.55 aα	1.55 aA	1.31 aα
	Cycle 4	3.83 aA	5.01 aα	6.22 aB	3.89 aα
	Cycle 5	2.18 aA	5.99 bα	3.27 aA	3.33 aβ
	Cycle 6	1.6 aA	1.92 aα	1.07 aB	1.16 aβ
Crop cycles 2 to 6 combined	Average	2.1 aA	3.4 bα	2.9 aA	2.5 aβ

3.4. Millet growth

3.4.1. Height

In both soils, when the height of the millet plants in infested soil was compared to that of sterilized soil, for each crop cycle independently, the difference was only significant for the 1st and 5th cycles (*table I*). The plants were higher in the sterilized soil. However, when the mean heights over crop cycles 2 to 6 combined were compared, the plants were not significantly higher in the sterilized soil than in the infested one, for both soils (*table I*).

On two occasions (1st and 3rd cycles), the millet in the infested fallow soil was significantly taller than that of the infested cultivated soil (*table I*) and never for the sterilized situation. Mean heights of crop cycles 2 to 6 combined showed a significant difference between height of millet in infested soils, but not in sterilized soils (*table I*).

3.4.2. Shoot biomass

Except for the 2nd cycle, the shoot biomass was significantly higher in the sterilized cultivated soil than in the infested one. For the fallow soil, this difference only appeared in half of the crop cycles (*table I*). When fallow and cultivated infested soils were compared, the shoot biomass was higher in the fallow soil but the differences were significant only for the 1st, 2nd and 3rd cycles. The same comparison for sterilized soils showed differences for the 3rd, 4th and 6th cycles. Statistical differences between crop cycles 2 to 6 combined were identical to those observed with heights (*table I*).

3.4.3. Root biomass

For half of the crop cycles, the root biomasses were significantly higher in the sterilized cultivated soil compared to the infested soil. In only one cycle (1st crop) in the fallow soil was the difference significant (*table I*). When sterilized or infested soil of both origins are compared, the root biomass has a tendency to be higher in the fallow infested soil, but the opposite is true for the sterilized soils. This last observation is confirmed by the comparison of the averages over crop cycles 2 to 6 combined (*table I*).

3.4.4. Pattern of plant responses

If the averages of crop cycle 2 to 6 combined (*table I*) are converted to a relative effect, expressed as

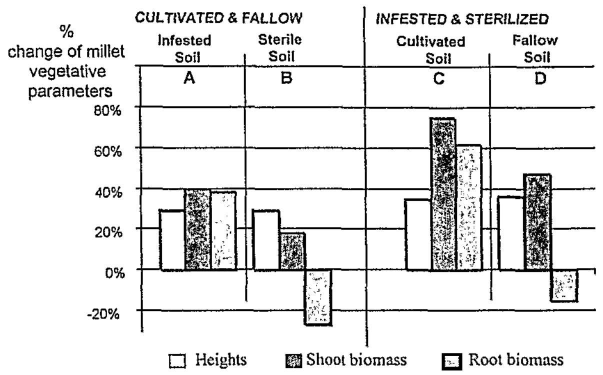

Figure 2. Beneficial effect on the millet vegetative characteristics (in %) resulting from fallowing or elimination of nematodes in the two types of soil, calculated from the average of the two to six crop cycles combined (*table I*): (A) effect of sterilization of cultivated soil; (B) effect of sterilization of fallowed soil; (C) effet of fallowing on an infested cultivated soil; (D) effet of fallowing on a sterilized cultivated soil.

a percentage, either for fallowing, or for eliminating nematodes by sterilization, the four patterns of plant response histograms have only two shapes (*figure* 2).

The comparison between fallow soil and cultivated soil, both infested by nematodes (equivalent to the field situation, *figure 2A*, *table I*: *I*, *III*) is similar to that obtained when comparing sterilized and infested situation of the cultivated soil (*figure* 2, *table I*: *I*, *II*), viz. all are characterized by a positive change in height, shoot and root biomass. The comparison between fallow and cultivated soil, both sterilized (*figure 2B*, *table I*: *II*, *IV*), is similar to that obtained when comparing sterilized and infested fallow soil (*figure 2D*, *table I*: *III*, *IV*), viz. shoot height and biomass also show a positive change, but the change in root weight is negative.

4. DISCUSSION

The objective of this work was to evaluate the impact of plant parasitic nematodes and of a fallow period on the growth of millet in a repeated cropping system. In this instance, we planted six crop cycles over 2 years, which simulated 6 years of millet crops in the Sudano-Sahelien zone where there is one cycle per year [21].

In the pots, the multiplication of nematodes was not obvious because the community did not increase in size at each cycle. Therefore, it could be argued that the pot experiment did not represent the field situation. The results suggest that this is not so. Firstly, living nematodes were present in both situations, because the extraction method only retrieves active individuals [19]. While nematodes can survive in anhydrobiosis for a long period without feeding in dry soil, they cannot survive for long in a moist soil [7]. It is therefore reasonable to assume that during the course of each cycle, the phytoparasitic nematodes were feeding on millet roots in the cultivated as well as in the fallow soil, without obvious differences in abundance. During the course of this experiment, there was no evidence of fungal or bacterial infection. Secondly, when the millet was grown in the cultivated soil, an increase of *S. cavernessi* was observed, as happens normally in millet fields in the region [11]. Thirdly, the growth of millet in the fallow soil was associated with the disappearance of *H. dihystera*. In the field, this species represents less than 2 % of the community [16]. Fourthly, by the 6th cycle, which corresponds to 6 years of crops in the field, the community was composed of a single endo- and a single ectoparasite, as is normally found in a field cultivated without interruption. In pots with fallow soil *P. pseudopratensis* was the only endoparasite present, whereas in the cultivated soil, as in the millet fields in Senegal, *S. cavernessi* was the only endoparasite. The widespread ectoparasite *T. gladiolatus* was the associated species in both soils. These four observations suggest that the soil environment in the greenhouse experiment was comparable, for both nematode and plant, to that in the field.

In the first crop cycle, there was a large increase in growth in the sterilized soil but this was expected [1, 13]. If this first crop is excluded, significant differences between infested and sterilized soil per cycle were rarely observed presumably because millet is not highly susceptible to nematode damage [2]. However differences could be detected if crop cycles were combined over time. Thus increasing the replicates from ten (one crop cycle) to about fifty (five crop cycles), which did not increase variability, makes the difference mathematically significant (*table I*) [17].

With or without nematodes, shoot growth of millet was always better when the plants were grown in fallow soil than in soil that was impoverished by repeated cultivation. However, the root system was smaller than in the cultivated, sterilized soil. This is presumably because a plant which has ready access to nutrients develops better but with fewer roots than one where there is a need to search for nutrients [20, 23]. This situation was not found in infested cultivated soil because the nematode community was probably pathogenic and reduced root growth. The fallow soil was itself infested by a large, but non-pathogenic nematode community, which did not affect the growth of the root system. This result is paradoxical, but is a typical response from a plant which increases the volume of its root system in reaction to nematode attack, as long as the latter does not destroy the new roots [25]. This reaction can also result in better development of millet [5].

If there was a non-infested field impoverished by many years of cultivation, fallowing would lead to an increase in millet development (*figure 2B*). The pattern of response of millet to fallowing (*figure 2A*, *B*) is the same as that obtained by the elimination of nematodes

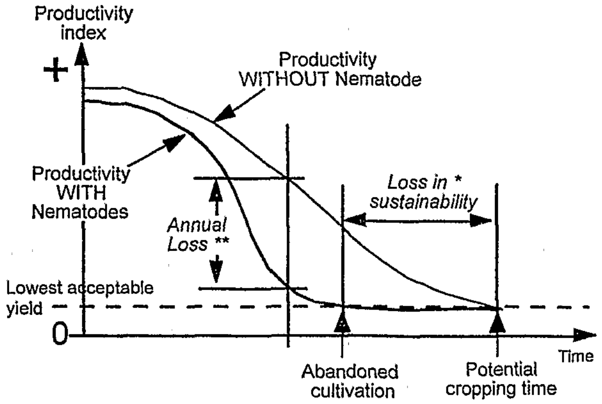

Figure 3. Estimated pattern of productivity of millet cultivated after fallow, with or without nematodes. ** Equivalent to nematicide response in one crop cycle; * equivalent to loss in cropping period due to early abandonment following inability of nematode infested roots to take up remaining nutrients.

in an infested fallow soil (*figure 2C, D*). But all soils are infested by nematodes. The classical practice of fallowing an impoverished infested soil, also led to an improvement in millet growth (*figure 2A*). In this realistic situation, the millet pattern of response would be equivalent to what the farmer could obtain if, instead of fallowing, he used a nematicide in the cultivated field (*figure 2C*) [3, 10].

Phytoparasitic nematode pressure increases with the length of cultivation at the same time as fertility decreases. Soil exhaustion and the impact of nematodes have common outcomes for the farmer: reduction of plant biomass and subsequent yield. As a consequence, both phenomena have usually been confused, minimizing the non-diagnostic effects of nematodes. In practical terms, the presence of nematodes leads to the farmer abandoning his field before soil fertility is exhausted (*figure 3*). This study, while undertaken under greenhouse conditions, confirmed that a fallow period is an efficient means of restoring soil fertility (as measured by the increase of millet growth), and eventually crop yield, as observed in the field. Parasitic nematodes limit yield of food crops in the Sudano-Sahelien region, but the results with millet suggest that it was not necessary to physically eliminate nematodes to control their pathogenic action; increasing nematode diversity by fallowing leads to a less pathogenic community in this environment.

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