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THE ROLE OF NEMATODES IN AGROECOSYSTEMS

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Each ecosystem consists of the three variables: active plant tissue, heterotrophs, and inactive organic matter. Heterotrophs are not simple parasites of autotrophs but they play a regulatory role in an ecosystem [21]. The regulatory function of heterotrophs is probably not adequately represented by standing crops or energy flow alone since even small changes in heterotrophs biomass can affect the equilibrium system. Nevertheless they are useful in many respects. Nematodes as heterotrophs are extremely rich in forms of trophic differentiations and they play surely regulatory function in natural ecosystems and in those created by man.

Agroecosystems are determined as efficient, artificially maintained ecosystems in early stages of succession and by this energy losses for respiration are small in relation to the biomass produced in the system [6]. In such systems a simple structure of plants is maintained by man,the animal world is less complicated and among soil microorganisms (this refers to cultivated fields) bacteria are predominant [23, 25]. They are also characterized by open matter circulation cycles. Agrocenoses, as relatively simple ecological systems, are characterized by small diversity and low, as a matter of fact, stability [19, 23]. Impact of man depends on simplification of structure at simultaneous intensification of matter cycling [23]. The intensification of agriculture still strenghthens the above features. A question arises how communities of soil nematodes, including plant nematodes, function in such specific ecosystems. The considerations will be refered mainly to cultivated fields of the temperate zone.

NEMATODES AGAINST SOIL FAUNA

Among soil invertebrates nematodes form a small fraction. To exemplify, it was established that nematodes in agroecosystems near Turew in Poland form 4.6% of total biomass of invertebrate fauna - this is a mean for rye and potato [12]. Still smaller values are for their share in total soil respiration, namely 0.08--1% [42], although their share in respiration of soil fauna amounts to 10-15% [28]. This does not denay that in cultivated soils the share of small invertebrates is a dozen or so times higher than that of large ones as related to the total metabolism of soil fauna [22]. The soil environment creates relatively stable living conditions for nematodes, although seasonal variability of numbers is clearly visible.

The role of this group of soil fauna in ecosystems can be analysed at different levels of organization such as an individual, population, species and community. It seems plausible to consider their role in a system analysis at the level of communities, differentiated in respect of trophy into first order consumers (phytophages), consumers of reducers (bacteriophages and mycophages), and consumers of higher orders (omnivores and predators).

DIFFERENTIATION OF NEMATODE COMMUNITIES WITHIN ECOSYSTEM TYPE

As an example, ecosystems in Poland are taken in which the differences in the structure and function of nematode communities characteristic for types of ecosystems such as forest, grassland and cultivated field, have been examined. Comparisons pertain to numbers, biomass, energy flow, and degree of complication of communities within types of ecosystems.

Total abundance of nematode communities is not a good measure of differentiating the ecosystem type. The range of numbers of nematodes found in agricultural ecosystems, amounting to 0.7-8.6 million individuals $\cdot$ m^{-2}, with fresh biomass of 0.2-3 g $\cdot$ m^{-2} [9, 34], have been also noted in other ecosystems.

The trophic structure of nematode communities shows differences between types of ecosystems. Averaged data from 30 ecosystems in Poland show that agroecosystems are distinguished by high numbers, biomass and respiratory metabolisms of bacterial feeders and plant feeders, whereas omnivores and predators are not numerous [33]. Similar observations can be found in the literature [2, 4, 9, 41]. From the trophic structure some characteristic relations come out between distinguished groups. They can be evidenced by comparing standing crop of numbers, biomass or respiratory metabolism of trophic groups. And so, the ratio of respiratory metabolism cumulated annually for bacterial feeders and fungivores to that of the remaining groups of nematodes excellently differentiates the types of ecosystems [33]. This ratio increases in a sequence grassland-forest-crop field ecosystems, illustrating clearly the significance of the group which feedes on destruent. Similar relations between omnivores and predators versus the remaining groups of nematodes point to insignificant role of this group in agroecosystems [33].

Mean weight of nematode individual excellently differentiates the main types of ecosystems [33]. In agroecosystems nematodes are smallest. Even within Tylenchida alone, cultivation treatments eliminated only large species [29]. It is known phenomenon that large saprophages disappear in agrocenoses [1]. The importance of this fact will be discussed later.

The genus diversity seems to be lover in agroecosystems than in other types of ecosystems [33]. Similar views are expressed by other nematologists [9, 42], and this is a congruent with a fact that diversity increase during the ecosystem development [20]. The generic diversity of nematodes within crop cultures turned to be smallest in root crops [38].

The fact of higher similarity of nematode communities within ecosystems of the same type is an evidence of dependence of biocoenotic structure on the ecosystem type [33]. It is typical that agrocenoses show higher similarity among them than the forest or grassland ecosystems. Within crop fields ecosystems that were examined the highest similarity of biocoenotic structure of nematode fauna was observed between root crops [38]. The type of culture turns to be a stucture creative factor for nematode fauna.

Production parameters of nematode communities are differentiated by the ecosystem type. If, for example, we consider consumption by nematodes in three types of ecosystems in Poland, it is apparent that the highest energy stream in agroecosystems reaches, via consumption, the bacterial and plant feeders [33]. The nematode community structure presented here for agroecosystems against natural or close-to-natural ecosystems can serve as an example of human impact on it. The effect of human activity within the ecosystem type can be also observed in the change of trophic and biocenotic structures of nematode fauna [40].

SIGNIFICANCE OF TROPHIC GROUPS

Bacterial feeders

This is actually a numerous group in agroecosystems. Its increased abundance is an effect of energy input to the ecosystem by man in the various form such as dung, other organic matter [31], and fertilizers, or by activation of energy resources in the ecosystem, such as drainage of fens on alder peat under conditions of the temperate climatic zone [13]. Response of bacterial feeders on organic manuring refers mainly to typical saprobionts (such as Rhabditis) and in smaller degree to the remaining bacterial feeders. It was estimated that bacteriophagous nematodes can cunsume 800 kg of bacteria/ha in one year [14]. The nematodes taking part in decomposition (that were studied by the author and thecolleagues using the method of exposure of bags with dead plant matter just in agrocenoses) can be useful for estimation of an index of energy flow between this matter and them as consumers of reducers. In one year nematodes consumed via bacterial production from [34] to 44% of organic matter decomposed by bacteria and fungi [35]. Such data were obtained in agroecosystems when postharvesting residues of barley together with roots were inserted to bags. Leaves and younger overground parts undergo decomposition much faster since 8.5 to 36.3% of organic matter decomposed by reducers reached nematodes during only [16] weeks [36]. These last estimates, as faced with evaluation of nematode share in the total metabolism of soil, point both to their regulatory role and to an important role in energy transfer between them as heterotrophs (in a broad sense of the word) and primary production.

The role of nematodes grazing on bacteria and fungal hyphae was judged by means of excellent experiments with microcosms reported in several compilation papers [3, 6, 44]. These experiments show that this group of nematodes enhances the release of nutrients, the rate of mineralization and turnover. In fact, nutrients are used both by producers and reducers, hence, one can speak about beneficial effect of nematodes on growth of plants. Therefore, the faster organic matter cycling in agrocenoses than in other ecosystems 24 results also from bacteriophagous nematodes. This also refers undoubtedly to mycophagous nematodes.

Both nematodes of the group of typical saprobionts (Rhabditidae), connected only with decaying organic matter, and representatives of Panagrolaimidae and Cephalobidae are considered as numerous bacterial feeders in agroecosystems. The role of the latter should be cleared up. They are able to colonize visually healthy plant tissues, penetrating inside them [7, 30], although their adaptation to parasitic life on plants is not documented yet, besides some fragmentary observations [15].

PLANT FEEDERS

There are numerous data proving that nematodes-parasites of higher plants are more numerous in cultivated soils than in uncultivated ones [7, 8, 11, 19]. The direct effect of plant feeding nematodes on higher plants is well known and there are many reviews of crop loss. There are also reports on stimulating effects of plant parasitic nematodes on growth of plant if they occur in small densities [5].

The role of phytophagous nematodes as consumers of primary production in ecosystems is little explored and hithero collected data are extremely controversial. Wasilewska [33] has estimated consumption by nematodes for 4.2% of root production in the rye culture and for 1.4% in the potato culture. Smolik [27] reported considerably higher values for grasslands.

There is a high diversity of environmental situations on which the actual effect of plant parasites on the cultured plant can depend. An example of ecological approach to such analisis are papers of Ferris V. R. et al. [10], Norton et al. [18], and Norton and Oard [17]. It may turn out in future that phytophagous nematodes (obligatory plant parasites included) will be considered, even for needs of evaluation of healthiness of crop cultures, in a feedback with other groups of nematodes. This pertains foremostly to the ratio of plant feeding nematodes to bacterial feeders, since it is though [43], that although phytophages decrease plant production, bacterial feeders stimulate it. This would be a compensation system in its action, triggered perhaps by pressure situation in the biocoenosis. However, the strength of this „compensative" reaction as well as overthreshold stimuli, that can this strength totally nihilate is unknown. Hitherto we have examples [40], that ecosystems with higher pressure of man show increased numbers of these two groups of nematodes. Agrotechnical treatments, through changes in feeding of plants, in degree of decomposition and mineralization, and in other soil processes, affect activity of both plant feeders and bacterial feeders [6]. The example that illustrates the effect of intensification of agriculture is used. The trophic structures of soil nematodes in potato culture of two regions in Poland 38 were compared. One culture was situated in western Poland, where agricultural landscape with water defficiency prevails. Potato fields was strongly manured, mechanically treated and included in a simplified crop rotation. On the contrary were cultures of potato in Mazurian landscape (lakeland), where a proximity of water catchment areas occurs and the crop rotation was longer at a similar level of fertilization. Most drastic differences between these two types of cultures were observed in plant feeding nematodes, including obligatory plant parasites, which were most numerous in the region of an intensive agricultural management. Exceptionally numerous occurrence of phytophages of the genus Paratylenchus was observed in another stress situation depending on drying up fens of alder peat origin [13, 37].

Omnivores and predators

Disappearance of omnivorous and predacious nematodes due to human activity is reflected in the literature. This process is considered even at present, as pointing to the degree of natural habitat deformation [9, 19, 29, 32, 39]. Disappearance of these nematodes at the pastures manured with sheep dung [31] and in the stress situation of drainage of fens of alder peat origin [40] are examples of the process in question.

Connections of omnivorous and predacious nematodes with natural environments or close-to-natural ones prove certain requirements towards the environment stability. The best evidence of this is low proportion of predators and omnivores in agrocenoses. Simultaneously, the fact of their occurrence in environment enhances probably the stability of biocenosis. The correlation, although only by using sta-

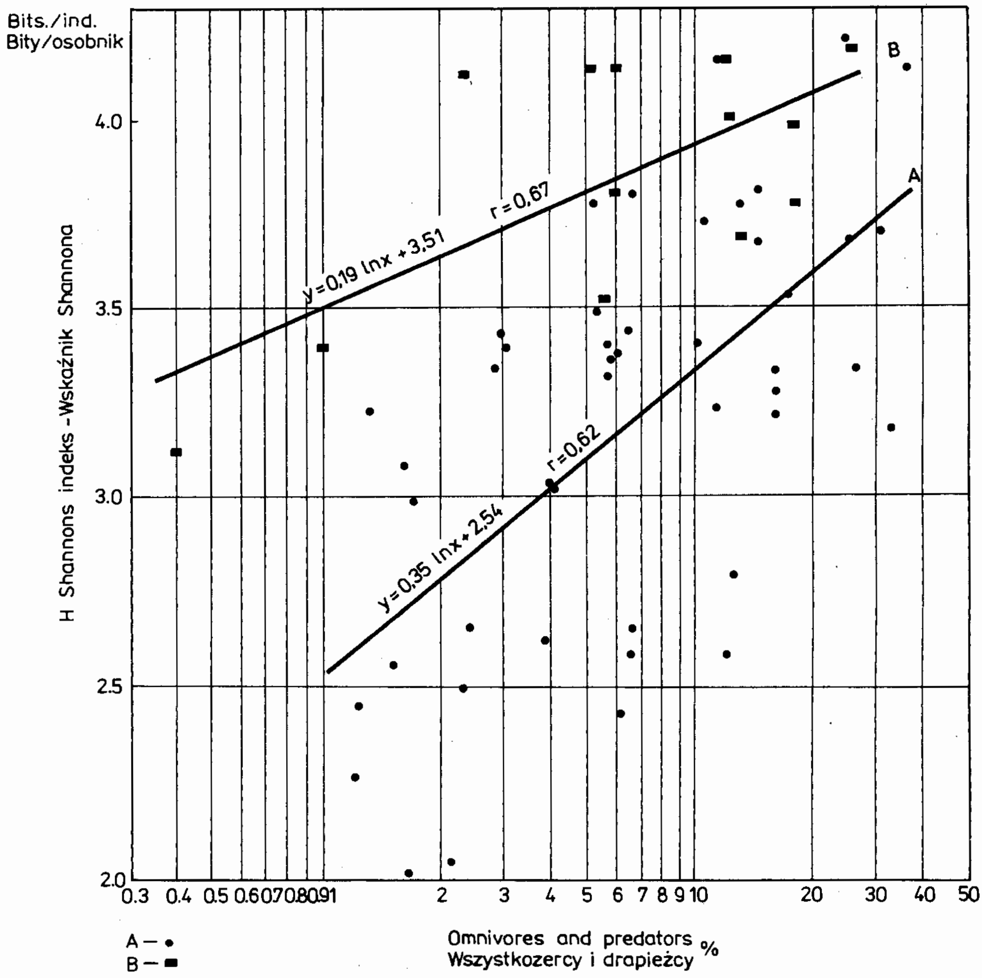

Fig. 1. Relationships between percentage of omnivores and predators in nematode community and the diversity index of whole nematode community;
A) agrocenoses in Mazurian region, Poland (α = 0.05) B) drainaged peat meadows of Biebrza river ancient valley, Poland (α = 0.01)

tistical method, can be shown between the omnivorous and predacious group (percent of share) and the diversity index in the whole nematode community (Fig. 1). One can, however, suppose that it is dependence of biological nature. A low index of diversity of the whole nematode community is characteristic for these ecosystems which reveal low percentage share of omnivores and predators. This dependence is less sharply drawn at high shares of omnivores and predators in the nematode community than at their low shares. Ecological characteristic of omnivores and predators (to which K-selective type of life strategy can be ascribed) and also their predacious or partly predacious mode of life, both account for elongation of the food chain in the habitat. Thus they play an important role in diminishing the rate of nutrient cycling in ecosystem. In such a sense they can increase the stability of the biocoenotic system.

FINAL REMARKS

The author of a classic paper on the role of nematodes in ecosystems [16] has devoted relatively little attention to agroecosystems. His data do not point to a proliferous development of plant feeding nematodes in crop cultures but dorylaimids occurred abundantly. Perhaps the paper of 1949 will serve as crucial point to which we will relate presently observed structures in our fields strongly influenced by man.

The increase of plant feeding forms, disappearance of predacious forms, minutization of fauna, enhancement of mineralization processes, acquisition of instability of the biocoenosis, all are the features that often accompany the strong impact of man on the natural environment. In the communities of nematodes under such situations the trophic structure is rebuilt (increase of plant parasites and bacterial feeders as well as decrease of omnivores and predators) and diminishing of species diversity and minutization of forms (thus faster rotation of matter in the system) are observed [40]. The impact of man brings about disappearance of species with lower costs of maintenance (among nematodes: omnivores and predators) and preference of groups of organisms characterized by high energy costs (among nematodes: bacterial feeders) which leads to faster mineralization of organic compounds. The proportions between thus distinguished functional groups of organisms determine the degree of adaptation of an ecosystem to mineral requisites in the environment. Thus the analysis of trophic structures in soil nematode community is a helpful tool for broader understanding of how ecosystems (agroecosystems included) function. Learning about the life history strategy of species and their groups initiated in nematology by a wonderful paper by Schiemer 26 will undoubtedly make a further step of this cognition process.

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ROLA NICIENI W AGROEKOSYSTEMACH

S t r e s z c z e n i e

Agroekosystemy charakteryzują się wysoką biomasą i wysoką aktywnością metaboliczną nicieni bakteriofagicznych. Średni ciężar ciała osobnika i różnorodność rodzajów nicieni obniża się pod wpływem zabiegów uprawowych. Liczebność bakteriofagów i mikofagów wzrasta pod ich wpływem dzięki dopływowi do gleby materii organicznej i nawozów. Nicienie mogą konsumować 800 kg/ha masy bakteryjnej w ciągu roku. Ilość skonsumowanej pośrednio poprzez bakterie i grzyby materii organioznej, rozłożonej z resztek pożniwnych jęczmienia, wynosiła 34-44%. Nicienie te zatem spełniają ważną rolę w przekazywaniu energii między autotrofami i heterotrofami, przyspieszając uwalnianie biopierwiastków zużywanych zarówno przez producentów, jak i reducentów. W glebach uprawnych są również liczne fitofagi. Ich wpływ na straty plonów jest dobrze znany, ale mało jest ocen ich konsumpcji. Konsumpcja fitofagów w uprawie ziemniaków wynosiła 1,4% produkcji korzeni, zaś w uprawie żyta 4,2%. Inaczej zachowują się wszystkożerce i drapieżce, których liczebność obniża się pod wpływem zabiegów uprawowych. Może to być miarą odkształcenia środowiska naturalnego i utraty stabilności, ponieważ łańcuch pokarmowy skraca się. Te nicienie mogą odgrywać ważną rolę w zmniejszeniu tempa krążenia biopierwiastków w ekosystemach i dlatego mogą zwiększać stabilność. Zabiegi uprawowe powodują zmianę struktury troficznej zespołu nicieni. Gatunki o niższych kosztach utrzymania (wszystkożerce i drapieżce) są zastępowane przez grupy gatunków o wyższych kosztach utrzymania (bakteriofagi). Prowadzi to do szybszej mineralizacji składników organicznych.

Л. Василевская

РОЛЬ НЕМАТОД В АГРОЭКОСИСТЕМАХ

Р е з ю м е

Агроэкосистемы характеризируются высокой биомассой и высокой метаболической активностью бактериофагических нематод. Средний вес тела одной особи и разновидность родов нематод снижаются вследствие агротехнических приемов. Численность бактериофагов с микофагами растет под их влиянием в результате поступления в почву органической материи и удобрений. Нематоды потребляют 800 кг/га/год бактерийной массы и косвенно, через бактерии и грибы 34-44% органической материи, образовавшейся после разложения послеуборочных остатков ячменя. Итак, эти нематоди выполняют важную роль в передачи энергии между автотрофами и гетеротрофами ускоряя освобождение биоэлементов, которые используются как продуцентами, так и редуцентами. Фитофаги также многочисленно выступают в сельскохозяйственных почвах. Ущерб, какой они причиняют урожаям, хорошо известен, но мало имеется данных по их потреблению. Консумпция фитофагов на культуре картофеля составляла 1,4% продукции корней, на культуре ржи - 4,2%. По-другому ведут себя всеядные и хищники, численность которых снижается вследствие агротехнических приемов. Можно это воспринимать, как степень деформации природной среды и потери стабильности, так как -происходит сокращение пищевой цепи. Обсуждаемые нематоды могут играть важную роль в снижении темпов круговорота биоэлементов в экосистемах и поэтому могут повышать стабильность экосистемов. Агротехнические приемы тянут за собой изменения трофической структуры нематод. Виды, характеризирующиеся низшими тратами на обмен (всеядные и хищники), заменяются группами видов, характеризующихся высшими тратами на обмен (бактериофаги), что в результате ведет к ускорению минерализации органических компонентов.