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NEMATODES OF THE DUNES IN THE KAMPINOS FOREST.

II. COMMUNITY STRUCTURE BASED ON NUMBERS OF INDIVIDUALS,
STATE OF BIOMASS AND RESPIRATORY METABOLISM

(Ekol. Pol. 19: 651-688). Quantitative analysis was made of a nematode community in the afforested dunes of the Kampinos Forest, taking the trophic groups of nematodes into consideration. This analysis was carried out in a successional sequence of dune working stations, from a dune with very scanty vegetation cover and low humus contents in the soil to a dune covered by an old tree stand, with dense vegetation cover and soil richer in humus.

The nematode population there was described by means of both their numbers and the state of their biomass. The seasonal variations in numbers and state of biomass were analysed in respect of the whole community and the various ecological groups. The influence exerted by the plant succession of the afforested dunes on quantitative relations between trophic groups of nematodes was determined. Calculation was made of respiratory metabolism of the nematode community on the basis of oxygen consumption measurements made by Overgaard Nielsen (1949).

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I. INTRODUCTION

The discussion of the species structure of nematodes inhabiting the afforested dunes of the Kampinos Forest (Wasilewska, 1970) is followed by the present publication dealing with quantitative analysis of communities, taking into consideration trophic groups of nematodes. This analysis was made, similarly to the first part of the study, in a successional sequence of dune working stations, from a dune very scantily covered with vegetation to dunes covered by an old tree stand and dense vegetation cover.

The data so far obtained on density and biomass of nematode communities in different habitats point to considerable differentiation of these values depending on the type of habitat. Table I contains values of density and biomass of nematodes in different habitats (forests, desert, grassland, cultivated land and others) established by Overgaard Nielsen (1949), Volz (1951), Banage (1963), Zlotin (1969a, 1969b), and also the author of this study, relating to areas in West and Central Europe and the steppe regions of the Soviet Union. Only the few authors who simultaneously investigated density and biomass have been cited.

Comparison of values in table I shows that natural habitats appear to be inhabited by nematodes to a greater degree than cultivated field habitats. It is nevertheless difficult to determine all the basic habitat factors which govern intensive occurrence of nematodes. The low density values in such natural habitats as semidesert steppe, poor dune regions and peat bogs suggest that the most important limiting factor is drought or excess humidity (that is, poorly aerated soil) or also minimum organic substance contents. Increase in readily decomposing organic substance leads to increase in microorganisms, which in turn provide increased food supplies for saprobiotic nematodes and nematodes feeding on fungi. This factor is therefore of a trophic nature. The second factor,

soil humidity, is physical in character: absence of free water in the soil and oxygen deficiency make it impossible for nematodes to lead an active life.

In connection with the statement made by Stöckli (1952), that readily decomposing organic substance determines the abundance of nematodes in the soil, and the statement by Overgaard Nielsen (1949) that their greater abundance is linked with more luxuriant vegetation cover, analysis was made of the effect of these two parameters on the nematode community in a successional sequence of dune working stations which in principle constituted one type of habitat. In a sequence of this kind the factors of vegetation cover and humus contents in the soil can be measured without difficulty and form a distinct gradient. These are simultaneously the two basic variable factors which may be decisive in relation to the occurrence of nematodes. The third factor – soil humidity, was correlated, in the given habitat, with increased vegetation cover.

The great majority of the present-day afforested areas in the lowland regions of Central Poland are situated on sandy soils, hence it is of great importance from both the theoretical and practical point of view to obtain a knowledge of the ecological processes taking place in the fauna of these soils as succession progresses in wooded regions. Analysis of nematode communities, taking into consideration division of the community into trophic groups may, in the case of the sequence examined, form an interesting contribution to this problem.

Seasonal variations in numbers and state of biomass of the community and the various ecological groups were analysed in the afforested dune habitat. The effect of the plant succession on the dunes on quantitative relations (numbers of individuals, state of biomass) between trophic groups was determined. These relations referred both to the percentages of numbers and biomass of the trophic groups and the rate of increase in number of individuals and biomass in the successional sequence of working stations. Finally calculation was made of the respiratory metabolism of the whole community and different trophic groups of nematodes, on the basis of data given by Overgaard Nielsen (1949). Information so far obtained on oxygen consumption by nematodes is in principle based only on material collected by this author. It was considered that, as he assumed, oxygen consumption by nematodes is an indicator of their food requirements and hence describes them from the trophic aspect.

II. STUDY AREA

The study area was described in the first part of the study (Wasilewska 1970). Readers are only reminded that six working stations in a dune area in the Kampinos Forest were chosen for the studies. Four of them (stations A, B, C and D) were situated on afforested dunes of considerable geo-

Numbers and state of biomass of nematodes in different habitats according to data given by various authors and my own data

Tab. I

Habitat	Numbers millions/m ²	Biomass g/m ²	Author	Sample depth
1) Habitat with herbaceous vegetation only				
Meadows (on mineral soils)	2-20	8-17.5	Overgaard Nielsen 1949, Denmark	5 cm
Pasture	10	14	- " -	5 cm
Grassland steppe	14.5	5.5	Zlotin 1969b, Soviet Union	?
True steppe	17	1.5	- " -	?
Dry steppe	5-13.4	1.6-3.8	- " -	?
Semi-desert steppe	1.1	0.7	- " -	?
<i>Corynephorus</i> slope, bare	0.175	1	Overgaard Nielsen 1949, Denmark	5 cm
<i>Corynephorus</i> slope, scattered vegetation	0.375	1	- " -	5 cm
<i>Corynephorus</i> slope, under <i>Calluna</i>	0.750	2	- " -	5 cm
2) Wooded habitat				
Beech wood	12.1	4.05	Volz 1951, Germany	25 cm
Oak wood	29.916	15.15	- " -	25 cm

Oak wood	6.2	1.46	Zlotin 1969b, Soviet Union	?
Mixed forest (<i>Potentillo albae-Quercetum</i>)	5	0.5	my own* Poland	25 cm
Dry pine forest (<i>Cladonio-Pinetum</i>)	2	0.2	— " —	25 cm
Afforested dunes	0.5-7	0.2-0.7	— " —	25 cm
3) Others				
Moorland	1.9-3.1	0.48-0.75	Banage 1963, England	6 cm
Moor (organic soils)	0.33-0.77	1-1.5	Overgaard Nielsen 1949, Denmark	5 cm
Coastal dune	1-2	2-2.5	— " —	5 cm
4) Cultivated fields under				
Rye	2.5	3	Overgaard Nielsen 1949, Denmark	5 cm
Wheat	3.5	0.56	Zlotin 1969b, Soviet Union	?
Turnip	1	0.7	Overgaard Nielsen 1949, Denmark	5 cm
a) Lucerne	2.75	non investigated	my own* Poland	
b) Lucerne together with nematodes living in plants	3.15	— " —	— " —	25 cm

*My own data constitute the annual average, maximum values are several times higher.

morphological similarity, and the vegetation covering them constituted a distinct successional sequence. These stations were arranged in a successional sequence in order of increasing humus content, age of the tree stand, degree of variety of species and degree of plant cover by vascular plants. The two remaining stations (*E* – mixed forest, *Potentillo albae-Quercetum* and *F* – dry pine forest, *Cladonio-Pinetum*) were not a direct continuation of the successional sequence formed by the preceding stations, but constituted two different variants of advanced succession in the dune areas of the Kampinos Forest and were included in the studies for purposes of comparison. A floristic description of the stations and their ecological characters is to be found in the first part of this study (Wasilewska 1970).

III. METHODS

The field sampling method, sample size and way used to extract nematodes have been described in the first part of this study (Wasilewska 1970). The materials presented in the present paper are based on samples taken in April, May, July, August and October 1968 and in February 1969. Abundance was determined on the basis of at least four repeats (25 ml of soil each) and state of biomass on two repeats (25 ml of soil each), for each working station and the given moment of time. The average numbers in the year for each of the stations were determined on the basis of at least 24 samples (6 months \times 4 repeats) and the average state of biomass in a year on the basis of 12 samples (6 months \times 2 repeats).

1. Division of nematodes into ecological (trophic) groups

The individuals found were segregated on the basis of literature dealing with ecological classification of nematodes (Overgaard Nielsen 1949, Paramonov 1952, 1962, 1964, Seinhorst 1961, Banage 1963, 1964, Winslow 1964 and Lee 1965), taking into consideration primarily the source of their food, into the following ecological (trophic) groups:

1. Microbivorous,
2. Fungivorous,
3. Parasites of higher plants,
4. Omnivorous,
5. Carnivorous (predators),
6. Food unknown.

The above division is very similar in general outline to that given by all the other authors; any differences are mainly in respect of either nomenclature, or

the degree of precision in differentiating the kind of food consumed. For instance Overgaard Nielsen (1949) distinguished only five groups (bacteria feeders, algae feeders, root suckers, predators and food unknown), and thus did not differentiate the fungivorous group. Paramonov (1952, 1962 and 1964), on the other hand, distinguished far more groups. Within the group termed here microbivorous he distinguished a group closely linked with the habitat of decaying organic residue, and a group which vegetates in healthy plant tissues. The character they have in common is their ability to feed on bacteria. It is not known, however, whether representatives of the latter are also capable of feeding on plant tissue as parasites. In some cases it would appear useful to treat these groups separately (Wasilewska 1967). The group of nematodes connected with plants was divided by Paramonov into several subgroups depending on their feeding habits, places in which they live and their effect on plants. In the present paper more detailed classification within the group of nematodes connected with higher plants is not necessary. Banage (1963, 1964) classified nematodes to the following groups: plant feeders, microbial feeders, miscellaneous feeders and predators, and thus did not distinguish the fungivorous group.

Classification of nematodes on the study stations was made on the basis of identification to genus and earlier knowledge of the species spectrum (Wasilewska 1970). Studies of this type, which are concerned with the general role of nematodes in soil ecology, can be carried out on a genus basis. Genera can be classified into ecological groups with a high degree of probability (Banage 1963, 1964, Sandner, Wasilewska 1970). Table II gives the genera for which representatives were found in the habitat analysed, classified in accordance with their appurtenance to an ecological group. It would thus seem necessary to give the reason for the way in which some of the genera have been allocated. For instance all representatives of the genus *Aphelenchoides* were allocated to the fungivorous group, as none of those species which are considered to be parasites of higher plants were found among them. No such subtle questions — such as the fact that *Aphelenhus avenae* proved in some cases to be a parasite of higher plants — were considered since the majority of the reports available refer to its fungivorous way of life. It must also be emphasised that the line of demarcation between the fungivorous group and group of parasites of higher plants is not very sharply defined. Evidence of this is provided by, for instance, the genus *Ditylenchus*, representatives of which can feed at the expense of higher plants and in some cases also on hyphae of fungi. The same probably applies to the genus *Tylenchus*. Therefore both obligatory and facultative parasites were allocated to the group of parasites of higher plants. Their importance in relation to plants differed greatly, but the source of their food is in both cases formed by plants, hence differentiation of the whole group is in this case sufficient.

Allocation of genera (found on study stations) to ecological groups

Tab. II

Microbivorous	Fungivorous	Parasites of higher plants	Omnivorous	Carnivorous (Predators)	Food unknown
<i>Acrobeloides</i> <i>Acrobelus</i> <i>Alaimus</i> <i>Anaplectus</i> <i>Cephalobus</i> <i>Cervidellus</i> <i>Chiloplacus</i> <i>Diplogaster</i> s.l. <i>Eucephalobus</i> <i>Euteratocephalus</i> <i>Heterocephalobus</i> <i>Panagrolaimus</i> <i>Plectus</i> <i>Rhabdolaimus</i> <i>Rhabditis</i> s.l. <i>Wilsonema</i> <i>Teratocephalus</i> <i>Zeldia</i>	<i>Apchelelenchoides</i> <i>Aphelenchus</i> <i>Nothotylenchus</i> <i>Paraphelenchus</i> <i>Deladenus</i>	<i>Aglenchus</i> <i>Boleodorus</i> <i>Ditylenchus</i> <i>Helicotylenchus</i> <i>Hemicycliophora</i> <i>Macroposthonia</i> <i>Malenchus</i> <i>Meloidogyne</i> <i>Nothocriconema</i> <i>Paratylenchus</i> <i>Pratylenchus</i> <i>Psilenchus</i> <i>Pseudhalenchus</i> <i>Rotylenchoides</i> <i>Rotylenchus</i> <i>Tetylenchus</i> <i>Trichodorus</i> <i>Tylenchorhynchus</i> <i>Tylenchus</i> <i>Xenocriconemella</i> <i>Xiphinema</i>	<i>Dorylaimellus</i> <i>Dorylaimoides</i> <i>Drepanodorus</i> <i>Eudorylaimus</i> <i>Mesodorylaimus</i> <i>Thornia</i> <i>Tylencholaimus</i>	<i>Jotonchus</i> <i>Mononchus</i> <i>Nygolaimus</i> <i>Tripyla</i>	<i>Cylindrolaimus</i> <i>Diphtherophora</i> <i>Monhystera</i> <i>Prismatolaimus</i>

The greatest difficulty in appurtenance was found in the case of representatives of genera of the order *Dorylaimida*, the majority of which were allocated here to the omnivorous group. Banage (1963, 1964) justifiably terms this group of nematodes "miscellaneous feeders". The lack of uniformity of this group is due to its containing species feeding at the expense of both lower and higher plants, and also on food of animal origin. There is no exact information on the food preferences of the majority of the species in this group or whether one given type of food preference occurs throughout the whole life period of the given species. Differentiation of this group was therefore based more on morphological similarity than on factual data for the various species. In general it may be said that creation of correct ecological classification of nematodes is a somewhat difficult task with the amount of knowledge so far available.

2. Determination of the body weight of nematodes and their biomass per unit of area

Determination of the body weight of nematodes presents considerable technical difficulty. The two studies to be found in literature on this subject refer to determination of weight by Overgaard Nielsen's (1949) and Andrassy's method (1956). If the body weight of nematodes given by these two authors are compared, in the case of species which can be identified with complete certainty, the results obtained by the two methods agree. Using Andrassy's method I determined the ranges of variations in body weight of several species analysed by these two authors, on the basis of measurements of body length and breadth cited by Meyl (1960). The key data given by Meyl are based on a large number of systematic and faunistic publications, hence the range of size of the species is wide. Table III illustrates the body weight of several species of nematodes determined by Overgaard Nielsen and Andrassy and

Body weight of several species of nematodes determined by Overgaard Nielsen and Andrassy and ranges of body weight determined by Andrassy's method on basis of body measurements of different populations cited by Meyl

Tab. III

Species	Weight in μg after Overgaard Nielsen	Weight in μg after Andrassy	Range of weight in μg
<i>Acrobeles ciliatus</i>	0.6	0.638	0.325–0.968
<i>Tylenchus davainei</i>	0.8	0.537	0.512–0.768
<i>Ditylenchus dipsaci</i>	0.9	0.794	0.473–2.503
<i>Plectus granulatus</i>	1	0.893	0.800–2.420
<i>Dorylaimus centrocerus</i>	3	2.112	1.200–2.701
<i>Dorylaimus longicaudatus</i>	5	7.589	4.159–18.225

the ranges of body weight determined by Andrassy's method on the basis of the body dimensions of different populations given by Meyl. The minimum weight of the species was from one to even five times smaller than the maximum. Hence the differences occurring in the findings of these two authors must be considered as due to the fact that they examined populations of the same species which differed in size. As the two methods were not in principle divergent I was able to use either of them.

In the present study the nematodes' body weight has been determined by means of the method described by Andrassy (1956), as it was considered technically simpler. Banage (1963) also applied this method for assessing the biomass of nematodes in moorland soils. Measurements of body length and breadth were made under a microscope (objective 40x) in a drop of water without a covering slide.

Comparison of average body weight of female and body weight per individual in a population of mixed age for several species, on the basis of sample taken in October 1969 on station D

Tab. IV

Species	Average body weight of female in μg	Weight per individual in a population of mixed in μg
<i>Rhabdolaimus terrestris</i>	0.053	0.047
<i>Cervidellus serratus</i>	0.098	0.036
<i>Monhystera villosa</i>	0.161	0.136
<i>Acrobeloides nanus</i>	0.165	0.070
<i>Panagrolaimus rigidus</i>	0.281	0.099
<i>Acrobeles ciliatus</i>	0.427	0.129
<i>Aphelenchus avenae</i>	0.429	0.086
<i>Tylencholaimus mirabilis</i>	0.669	0.164
<i>Paraphelenchus pseudo-parietinus</i>	0.761	0.069
<i>Tripyla affinis</i>	1.413	1.160

In order to determine the nematodes' biomass per unit of area on the given working station at a given moment of time calculation was made of the body weights of all individuals from two samples (each 25 ml of soil) obtained from mixing 20 samples taken under field conditions. Each of the samples corresponded to a cylinder of soil with a base 1 cm^2 and height 25 cm. The mean values from these samples were used for calculations of the state of biomass per larger units of area.

The state of biomass on a given station was thus determined as the sum total of weights of all the individuals currently occurring in samples. The same procedure was used for samples throughout the study period. Although

this was laborious it gave a true picture of the biomass of the community. Calculations of average body weight of an adult individual of a given species multiplied by its numbers introduced considerable error, as is shown by comparison of the average body weight of one female and body weight per individual in a population of mixed ages in the same sample (Tab. IV). In the case of the species *Paraphelenchus pseudoparietinus* differences between weights were more than tenfold.

IV. SEASONAL VARIATIONS IN NUMBERS AND BIOMASS OF NEMATODES

Seasonal variations in numbers and state of biomass were analysed on the four working stations given the letters A, B, C and D, and arranged in a gradient of increasing vegetation cover and increasing humus content.

The curve of variations in total numbers of soil nematodes in a dune habitat exhibited two peaks during the course of a year (Fig. 1a). This two-peak course is thus characteristic both of the natural habitat analysed and of cultivated field habitats (Winslow 1964, Szczygieł 1966, Kozłowska 1967, Wasilewska 1967). Main peaks of numbers are most frequently observed in spring and autumn, while minima are connected with the summer drought period and period of low winter temperatures. In spring and autumn temperature and precipitation relations create optimum conditions for the nematodes' development. Many authors also connect periods of maximum numbers with the vegetation growth period (Yeates 1968).

In the afforested dune habitat examined the course taken by abundance and biomass dynamics was clearly correlated with the course of the atmospheric precipitation curve (Fig. 1). Maximum rainfall and maximum numbers occurred at the beginning of July and in October. It was only on the station with the most luxuriant vegetation cover (station D)

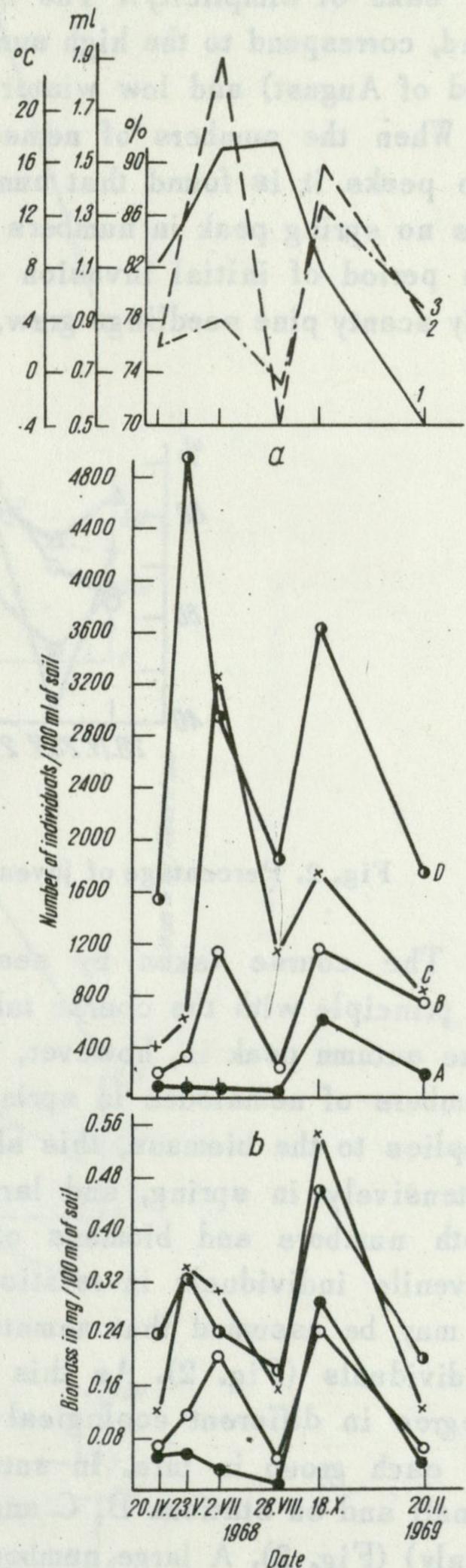


Fig. 1. Seasonal variations in numbers (a) and biomass (b) of whole nematode community on four working stations
1 - air temperature (monthly average),
2 - rainfall (monthly average), 3 - relative atmospheric humidity (monthly average)

that peak numbers occurred earlier, namely at the end of May (not only the May peak but also the early July peak have been termed „spring peak” for the sake of simplicity). The minima of numbers of nematodes, on the other hand, correspond to the high summer temperature with simultaneous low rainfall (end of August) and low winter temperature (February).

When the numbers of nematodes are compared during the periods of the two peaks it is found that numbers are higher in spring than autumn. There was no spring peak in numbers on station A, most probably because in spring the period of initial invasion of plants on the almost bare dune, on which only scanty pine seedlings grew, had only just begun.

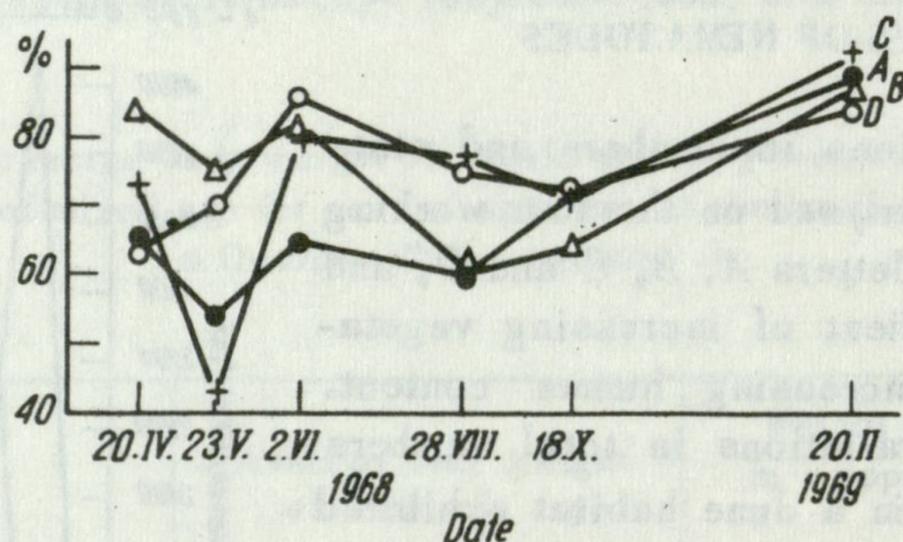


Fig. 2. Percentage of juveniles in relation to whole nematode community

The course taken by seasonal dynamics of nematode biomass agrees in principle with the course taken by seasonal dynamics of numbers (Fig. 1b). The autumn peak is, however, far higher than the spring one. Therefore if the numbers of nematodes in spring are higher than in autumn, while the reverse applies to the biomass, this shows that small forms of nematodes occur more intensively in spring, and larger forms in autumn. In February, i.e. winter, both numbers and biomass of nematodes decreased. As the percentage of juvenile individuals in relation to total numbers was very high in February it may be assumed that nematodes overwinter mainly in the form of juvenile individuals (Fig. 2). As this phenomenon does not take place to a uniform degree in different ecological groups it will be discussed during the review of each group in turn. In autumn (October) the percentage of juveniles was small and on stations B, C and D was far smaller than during the spring peak (July) (Fig. 2). A large number of the imaginal individuals existing in autumn must therefore die during the late autumn or winter period.

The seasonal dynamics of numbers and state of biomass in the various ecological groups differ from each other chiefly in respect of size of peaks. The microbivorous group exhibits considerable fluctuations in abundance during the year (Fig. 3). Seasonal variations in the state of biomass of this

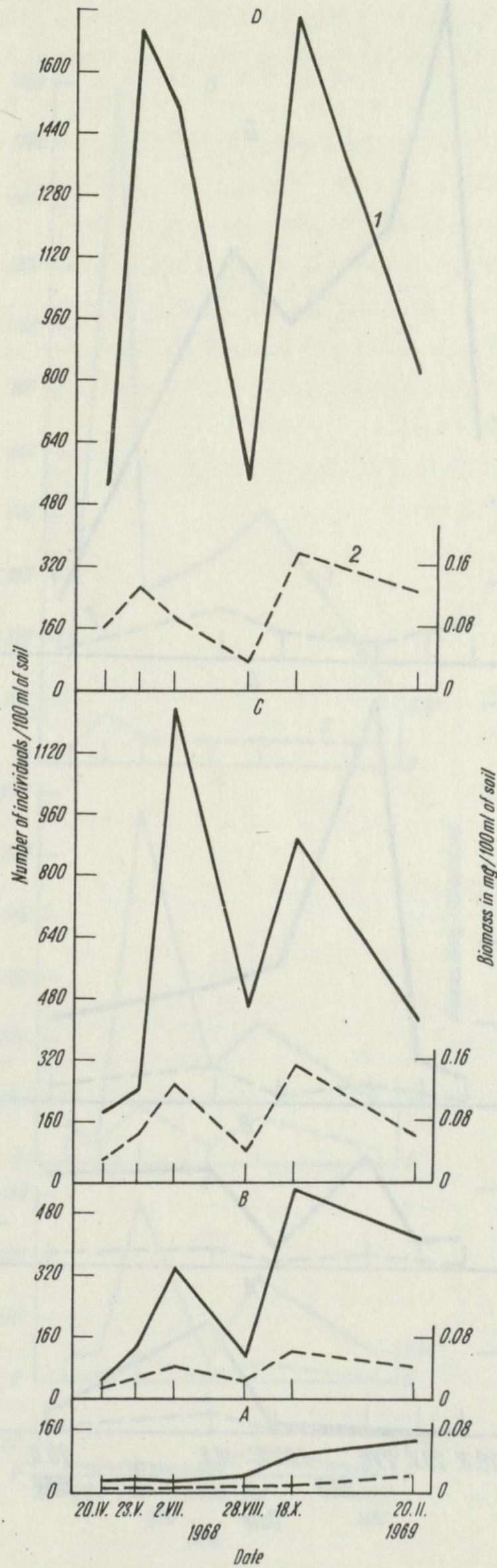


Fig. 3. Seasonal variations in numbers and biomass of microbivorous group on stations A, B, C, D
 1 - numbers, 2 - biomass

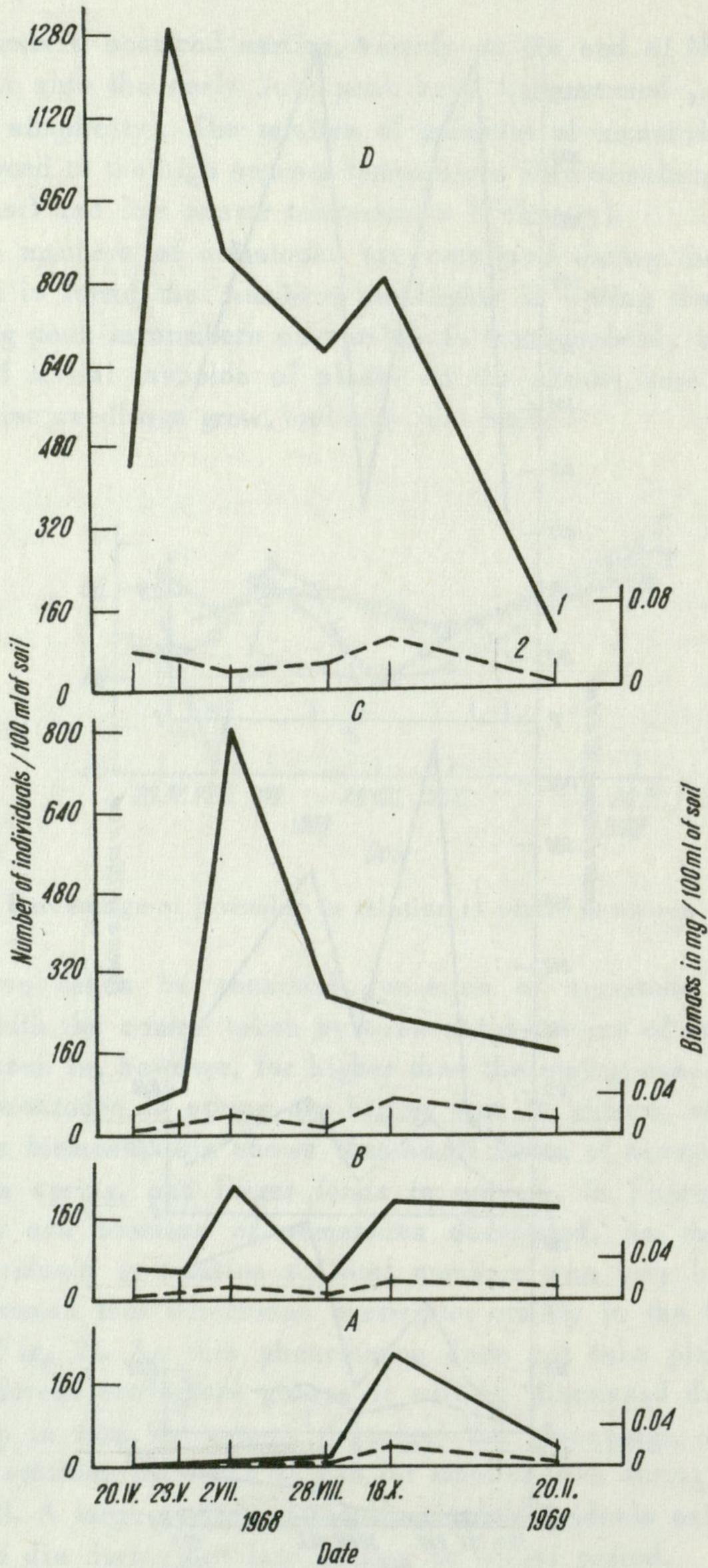


Fig. 4. Seasonal variations in numbers and biomass of fungivorous group on stations A, B, C, D
 1 - numbers, 2- biomass

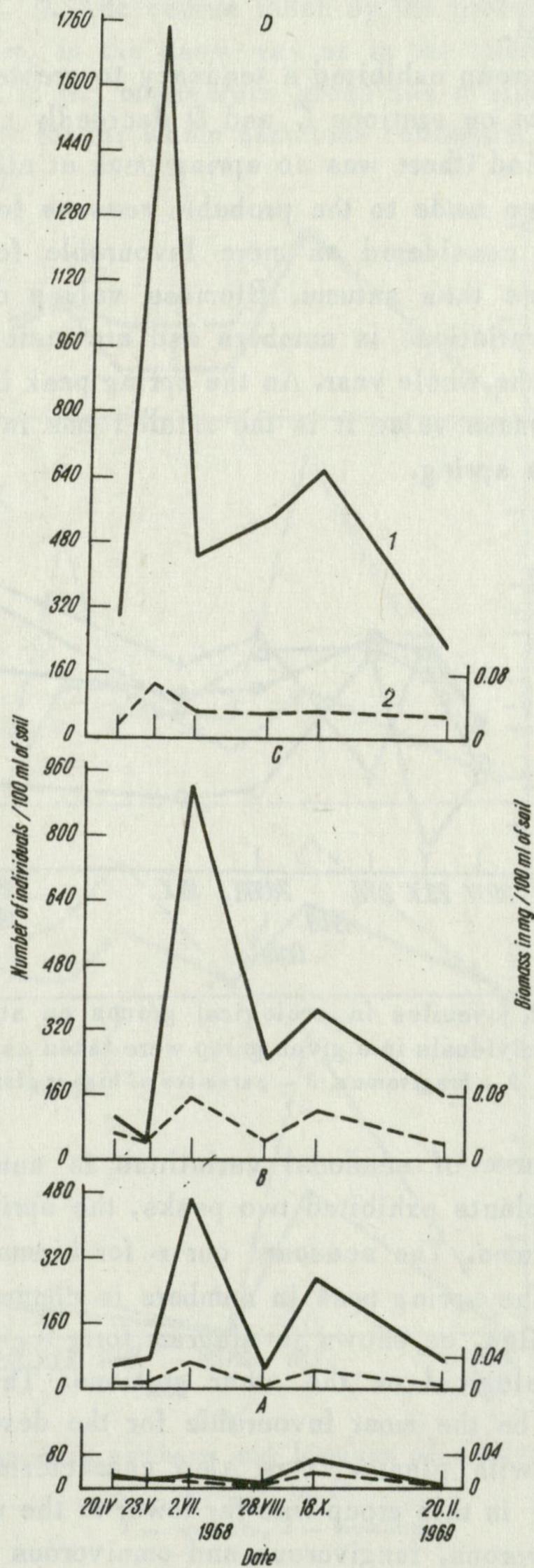


Fig. 5. Seasonal variations in numbers and biomass of group of parasites of higher plants on stations A, B, C, D
1 - numbers, 2 - biomass

group follows the same pattern as the numbers. In winter, although numbers appear to be reduced in relation to the autumn peak, they are maintained on a relatively high level.

The fungivorous group exhibited a tendency to greater abundance in spring on station *B*, whereas on stations *C* and *D* decidedly maximum numbers were found during this period (there was no spring peak at all on station *A* – reference has already been made to the probable reasons for this) (Fig. 4). This period can thus be considered as more favourable for the development of fungivorous nematodes than autumn. Biomass values during the season are not proportional to variations in numbers and are maintained on a relatively low level throughout the whole year. As the spring peak in numbers corresponds to relatively low biomass value it is the small forms in the fungivorous group which predominate in spring.

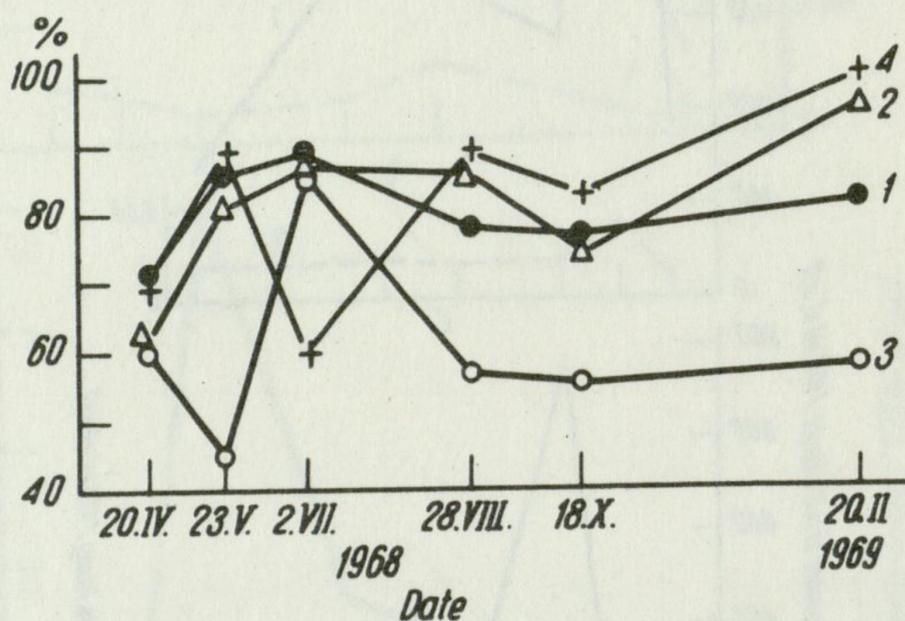


Fig. 6. Percentage of juveniles in ecological groups on station *D*. Numbers of all individuals in a given group were taken as 100%

1 – microbivorous, 2 – fungivorous, 3 – parasites of higher plants, 4 – omnivorous

Although the curve of seasonal variations in numbers in the group of parasites of higher plants exhibited two peaks, the spring peak was decidedly greater than the autumn. The seasonal curve for biomass exhibited a similar tendency (Fig. 5). The spring peak in numbers is connected with the maximum percentage of juveniles, as shown in diagram form for station *D* (Fig. 6), the situation being analogical on the other stations. The spring period would therefore appear to be the most favourable for the development of nematodes directly connected with plants. It is also characteristic here that the percentage of juveniles in this group was far lower in the winter month (February) than in the microbivorous, fungivorous and omnivorous groups. This is shown in diagram form for station *D* (Fig. 6). Thus the conclusion given above that nematodes overwinter mainly in the form of juveniles applies primarily to the microbivorous, fungivorous and omnivorous groups, and to a far lesser extent to the parasites of higher plants.

Two peaks were also observed in the seasonal curve of numbers for the omnivorous group (Fig. 7). The course taken by the biomass curve corresponds to the curve of numbers, in the same way as in the microbivorous group. The high individual weight in the omnivorous group has a significant effect on the absolute biomass values for the whole nematode community.

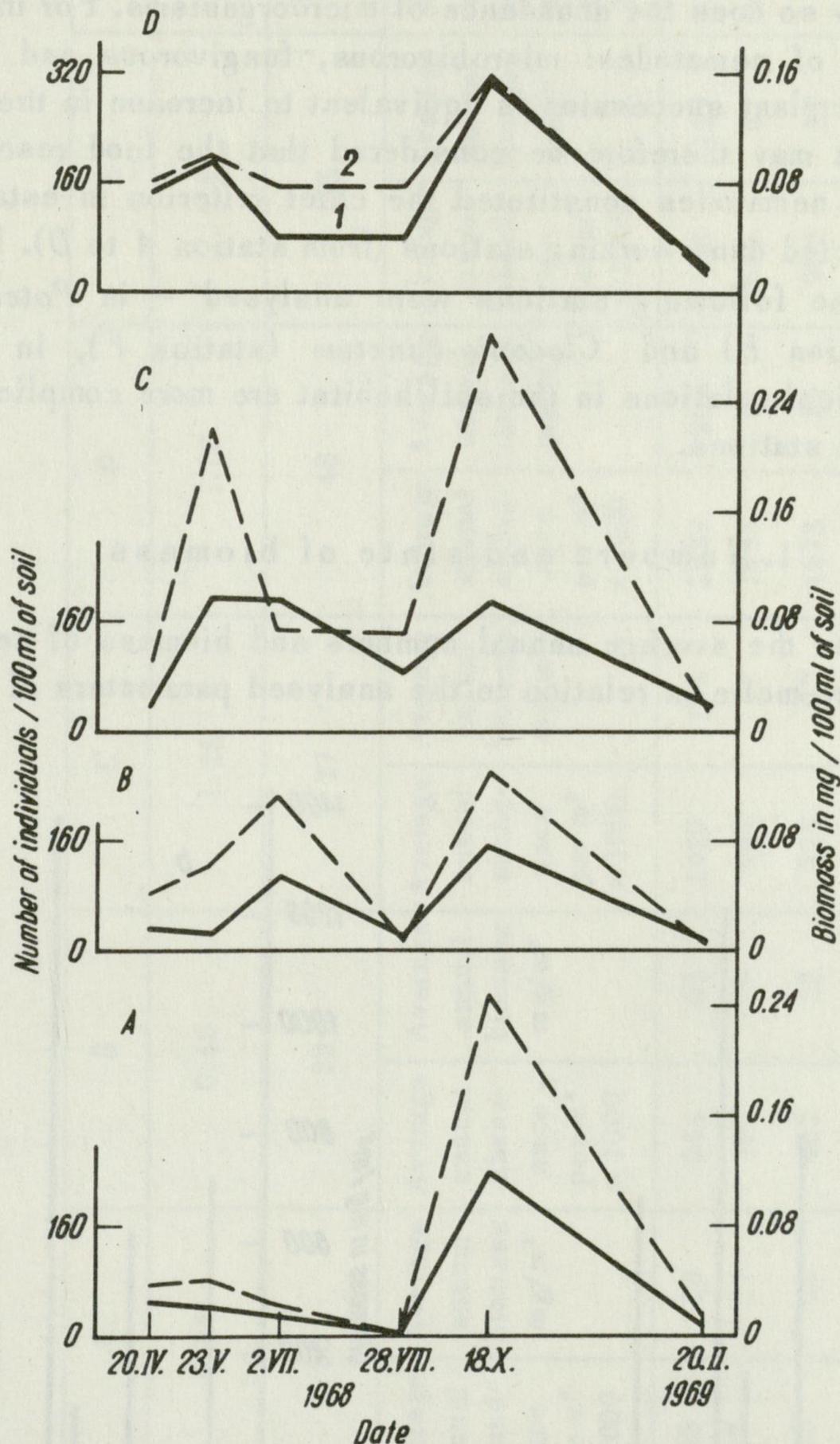


Fig. 7. Seasonal variations in numbers and biomass of omnivorous group on stations A, B, C, D

1 - numbers, 2 - biomass

Seasonal variations in the numbers of predators were not taken into consideration on account of the low numbers of this group.

V. INFLUENCE OF PLANT SUCCESSION OF THE DUNES ON THE NEMATODE COMMUNITY

As the plant succession on the afforested dunes progresses, the root mass of both herb layer plants and trees and also humus contents increase in the soil, and probably so does the abundance of microorganisms. For the three most numerous groups of nematodes: microbivorous, fungivorous and parasites of higher plants, the plant succession is equivalent to increase in the food supply of the habitat. It may therefore be considered that the food resources of the habitat for these nematodes constituted the chief criterion in establishing the order of the selected dune working stations (from station *A* to *D*). For purposes of comparison the following stations were analysed – in *Potentillo albae-Quercetum* (station *E*) and *Cladonio-Pinetum* (station *F*), in which both trophic and physical relations in the soil habitat are more complicated than on the previous dune stations.

1. Numbers and state of biomass

Table V gives the average annual numbers and biomass of nematodes calculated per square metre in relation to the analysed parameters of the stations.

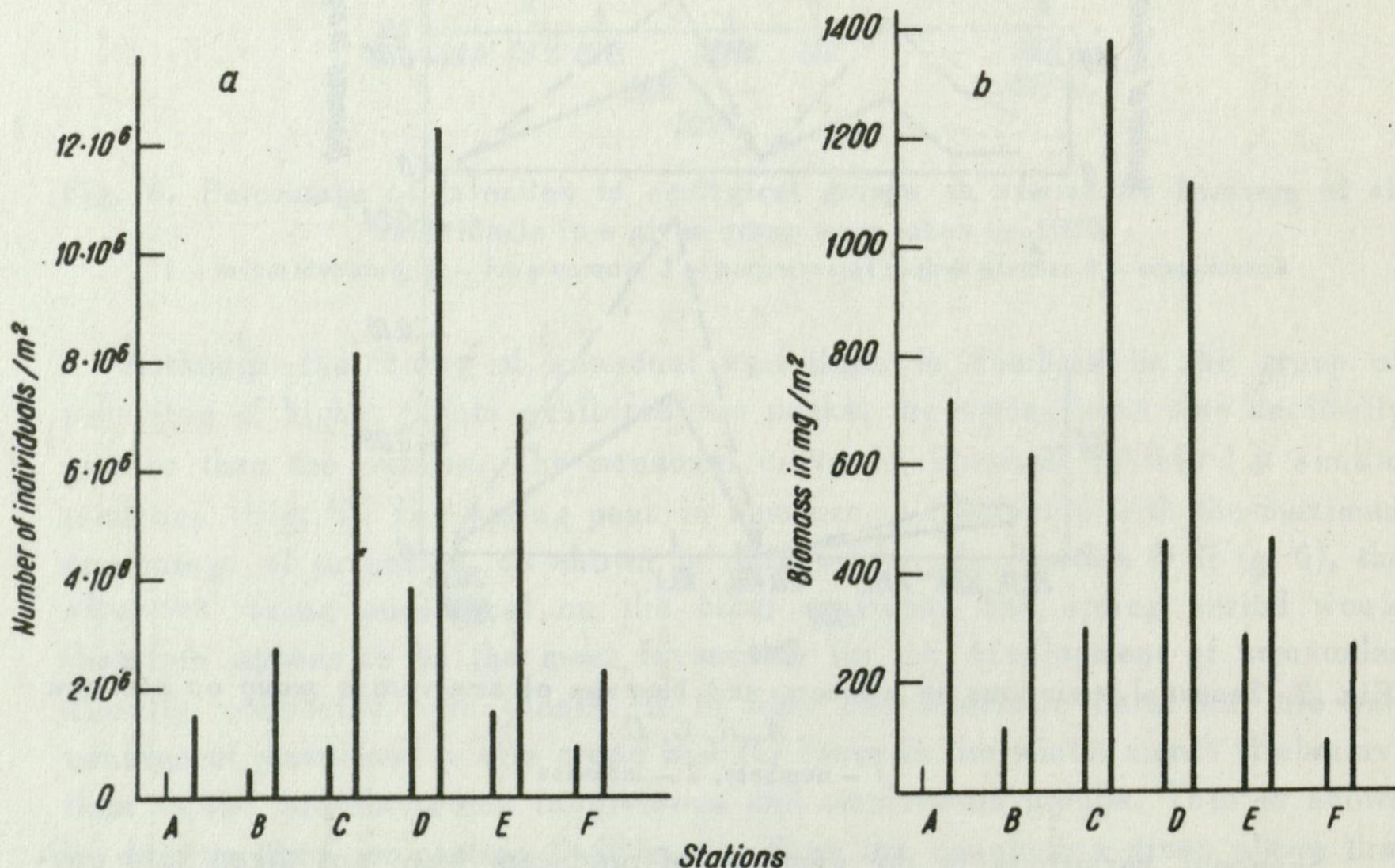


Fig. 8. Maximum and minimum *a* – numbers and *b* – state of biomass found during period from April 20th 1968 to February 20th 1969 on each station

Numbers and state of biomass of different ecological groups of nematodes in the successional sequence of dune working stations

Tab. V

Working station	A		B		C		D		E		F	
% of humus in soil	0.24		0.40		1.25		1.58		2.13		2.29	
% of vascular plant cover	10		22		27		48		55		10	
Group	Average annual abundance per m ² × 1000	Average annual biomass mg/m ²	Average annual abundance per m ² × 1000	Average annual biomass mg/m ²	Average annual abundance per m ² × 1000	Average annual biomass mg/m ²	Average annual abundance per m ² × 1000	Average annual biomass mg/m ²	Average annual abundance per m ² × 1000	Average annual biomass mg/m ²	Average annual abundance per m ² × 1000	Average annual biomass mg/m ²
Microbivorous	138	20	644	83	1420	194	2839	268	1468	129	903	85
Fungivorous	117	11	326	25	669	32	1935	81	1665	32	479	21
Parasites of higher plants	65	20	412	32	772	97	1673	86	962	52	499	29
Omnivorous	152	150	145	150	305	300	350	213	190	104	49	56
Predators	0	0	19	16	38	36	38	34	40	52	0	0
Food unknown	8	1	30	2	88	6	110	9	105	8	20	1
Total	480	202	1576	308	3292	665	6954	691	4430	377	1950	192

Calculation of the average annual numbers and biomass were based on samples taken in six periods. The differences between the maximum and minimum numbers and biomass found for each of the stations depending on the season are illustrated by figures 8a and b.

Numbers and state of biomass of the whole nematode community and of the various ecological groups increased almost regularly from station A to D (Tab. V). This increase was thus dependent on the food resources of the habitat. On station E in *Potentillo albae-Quercetum*, despite the higher humus contents and greater plant cover than on station D, the level of numbers and biomass was lower. While considering *Potentillo albae-Quercetum* as the most advanced successional stage of the afforested dunes in the Kampinos Forest, it must be emphasised that the numbers of nematodes in the habitat were not the maximum numbers found. The species structure of nematodes on this station was, however, similar to that on stations C and D (Wasilewska 1970). On station F (*Cladonio-Pinetum*) the numbers and state of biomass were lower than in *Potentillo albae-Quercetum* and lower than on stations C and D. It is very likely that the differences in the abundance of soil microflora are responsible for the fact that the numbers of nematodes on stations E and F are smaller than on the other stations. The data given by Jakubczyk (1968) referring to the Kampinos Forest show that the abundance of microflora was almost twice higher on the dune with scanty vegetation than in a mixed forest, (*Pino-Quercetum*) and in dry pine forest, (*Cladonio-Pinetum*).

2. Percentage of ecological groups in the nematode community

The working stations were compared in respect of the structure of the nematode community. This was done by taking into consideration the percentages of the previously distinguished ecological groups, assuming the average numbers of individual nematodes collected on a given station during the study period as 100% (Fig. 9a). Percentages were established in a similar way on the basis of biomass (Fig. 9b). The percentages of numbers show that the groups of microbivorous, fungivorous and parasites of higher plants can be considered as forming the core of the whole community of nematodes. The percentages of biomass, however, show that the omnivorous and microbivorous groups predominate in comparison with the group of higher plant parasites and the fungivorous group. Consideration of relations between ecological groups of nematodes is thus far more complete when it is based on both numbers and biomass.

The most characteristic feature of the nematode community structure is the increase in the percentage of biomass and the tendency to increase in the

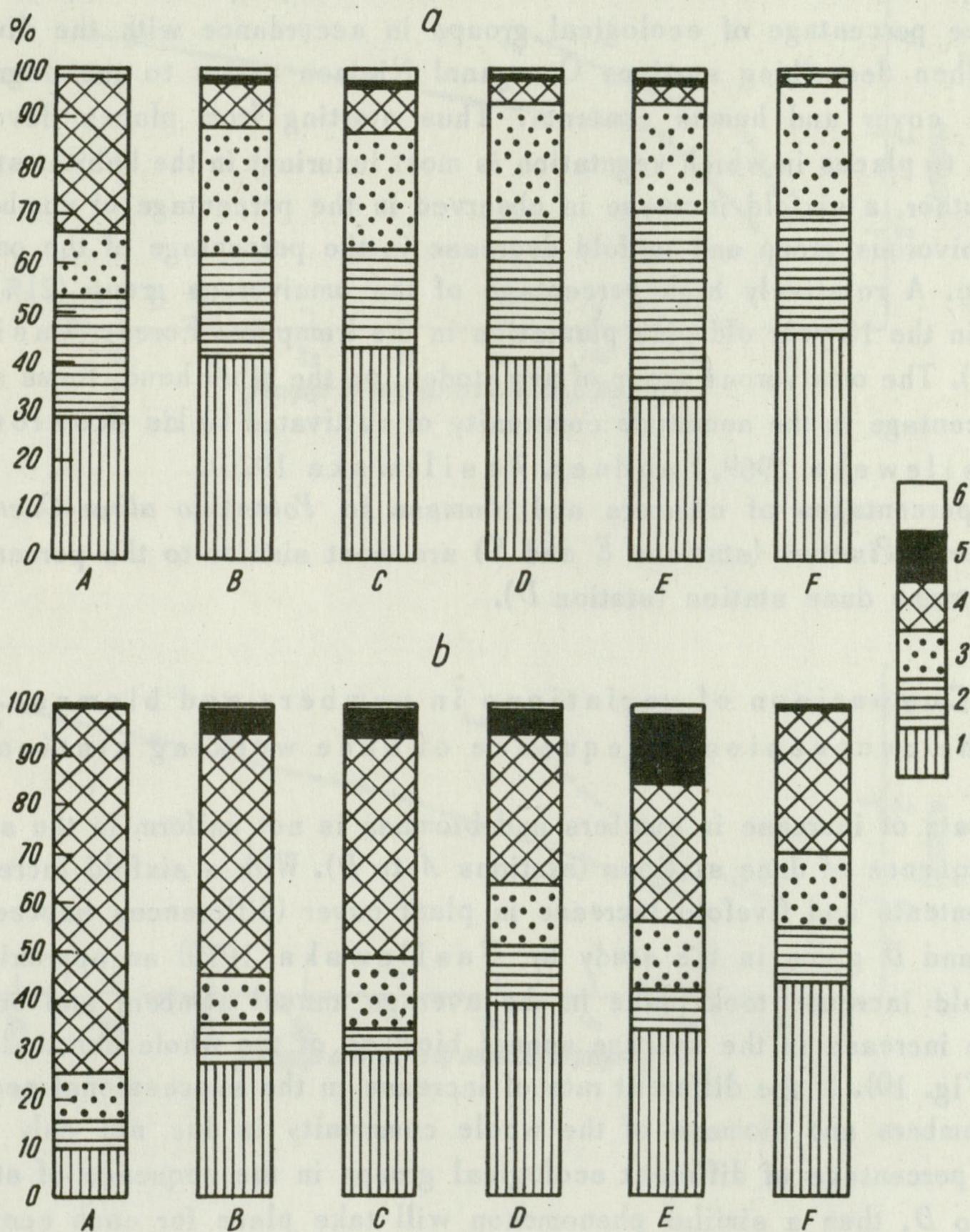


Fig. 9. Percentage of ecological groups calculated on basis of mean annual numbers — *a* and mean annual biomass — *b*

1 — microbivorous, 2 — fungivorous, 3 — parasites of higher plants, 4 — omnivorous, 5 — predators, 6 — food unknown

percentage of numbers of the microbivorous group, and the decrease in the percentage of biomass and numbers of the omnivorous group in the successional sequence of four dune stations (from station *A* to *D*). A similar relation can be gathered from the studies by Overgaard Nielsen (1949). Using the data

contained in the monograph by this author on p. 27–29 and in table V, referring to the sequence of stations in the habitat termed *Corynephorus* slopes, I calculated the percentage of ecological groups in accordance with the division I used. When describing stations Overgaard Nielsen refers to the degree of vegetation cover and humus contents. Thus starting from places devoid of vegetation to places in which vegetation is most luxuriant in the habitat studied by this author, a sixfold increase is observed in the percentage of numbers of the microbivorous group and tenfold decrease in the percentage of the omnivorous group. A relatively high percentage of the omnivorous group (21%) was observed in the 15-year old pine plantation in the Kampinos Forest (Wasilewska 1971). The omnivorous group of nematodes, on the other hand, forms a very small percentage in the nematode community of cultivated fields (Kozłowska 1967, Wasilewska 1969, Sandner, Wasilewska 1970).

The percentages of numbers and biomass in *Potentillo albae-Quercetum* and *Cladonio-Pinetum* (stations *E* and *F*) are most similar to the percentages of the extreme dune station (station *D*).

3. Comparison of variations in numbers and biomass in the successional sequence of dune working stations

The rate of increase in numbers and biomass is not uniform in the successional sequence of dune stations (stations *A* to *D*). With a sixfold increase in humus contents and fivefold increase in plant cover (differences between stations *A* and *D* given in the study by Wasilewska 1970) an approximately fourteenfold increase took place in the average annual numbers and only 3.4 times the increase in the average annual biomass of the whole nematode community (Fig. 10). If the different rate of increase in the successional sequence of the numbers and biomass of the whole community is due not only to the different percentage of different ecological groups in the sequence of stations from *A* to *D*, then a similar phenomenon will take place for each ecological group. The group of microbivorous nematodes exhibits a nineteenfold increase in numbers and only 8.3 times the increase in biomass, if stations *A* and *D* are compared (Fig. 11). Analogically the fungivorous group exhibits 16.5 times the increase in numbers and only 7.3 times the increase in biomass (Fig. 12); the group of parasites of higher plants – almost 26 times the increase in numbers and only 4.4 times the increase in biomass (Fig. 13) and the omnivorous group, where the differences are smallest, almost 2.5 times the increase in numbers and 1.5 times the increase in biomass (Fig. 14).

The different rate of increase in numbers and biomass is not due to the increasing percentage of juvenile forms (smaller forms) in the sequence of stations from *A* to *D*. The percentage of juvenile forms is not a consecutive

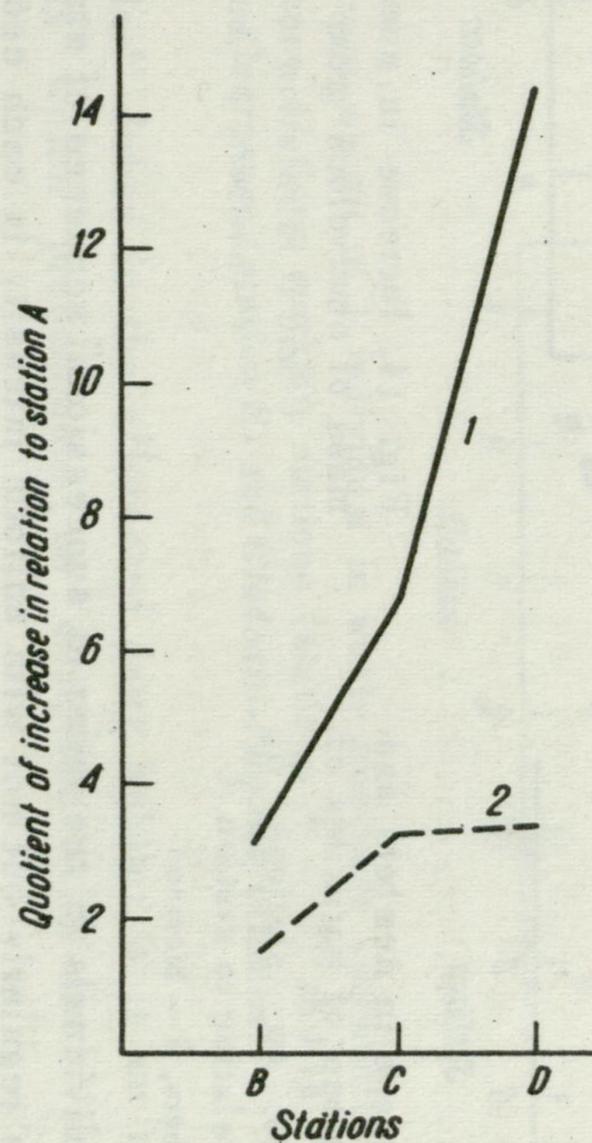


Fig. 10. Increase in numbers and biomass of whole nematode community on stations B, C and D in relation to station A
1 - numbers, 2 - biomass

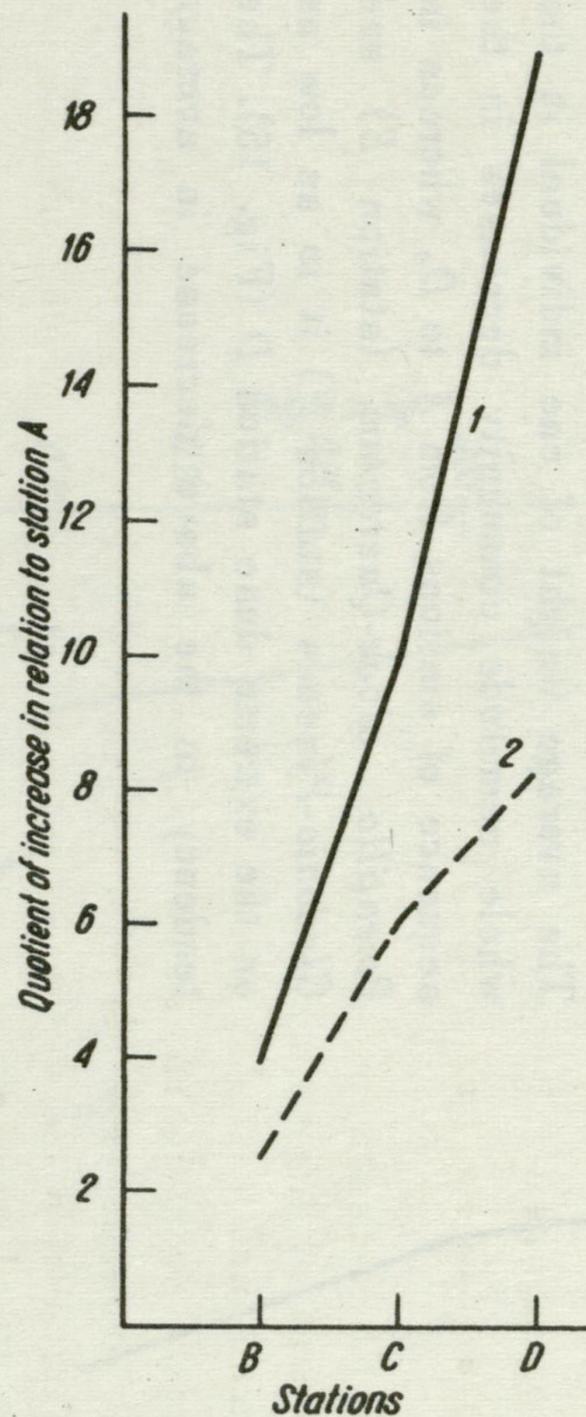


Fig. 11. Increase in numbers and biomass of microbivorous group on stations B, C and D in relation to station A
1 - numbers, 2 - biomass

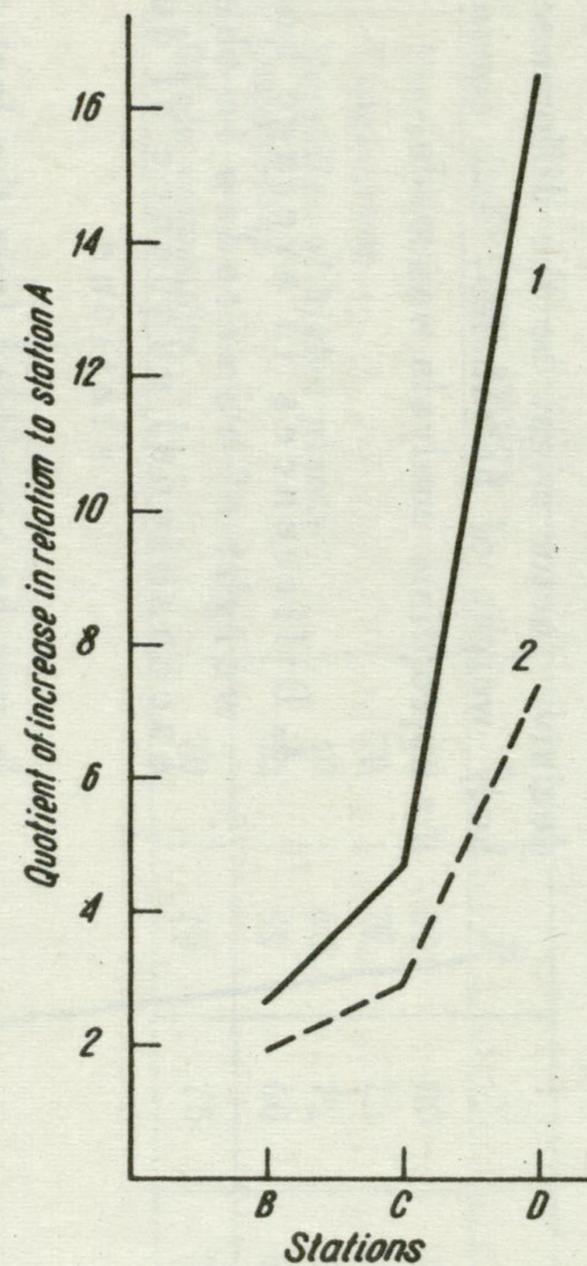


Fig. 12. Increase in numbers and biomass of fungivorous group on stations B, C and D in relation to station A
1 - numbers, 2 - biomass

sequence in the line of stations from *A* to *D* (Tab. VI), hence it is not this which decides the differences in the rate of increases referred to above. The decisive factor might be the difference in the body weight of nematodes, and consequently the appropriate analysis was made.

4. Differences in average body weight of nematodes in the successional sequence of dune stations

It may be concluded from the fact that the rate of increase in numbers of individuals is greater than the rate of increase in their biomass in the successional sequence of dune stations, that there is a decrease in the average body weight of individuals in this sequence. The average weight of one individual in the whole nematode community decreases in the sequence of stations from *A* to *D*, whereas in *Potentillo albae-Quercetum* (station *E*) and *Cladonio-Pinetum* (station *F*) it is as low as on the extreme dune station *D* (Fig. 15). The tendency to the above decrease in average

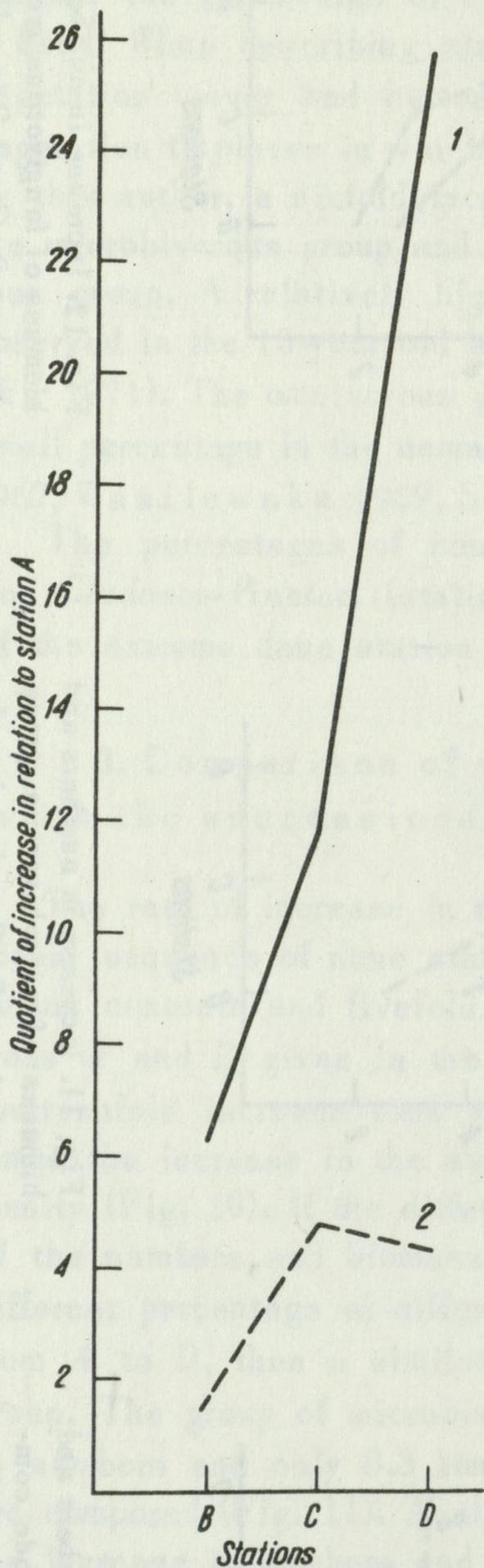


Fig. 13. Increase in numbers and biomass in group of parasites of higher plants on stations *B*, *C* and *D* in relation to station *A*
1 - numbers, 2 - biomass

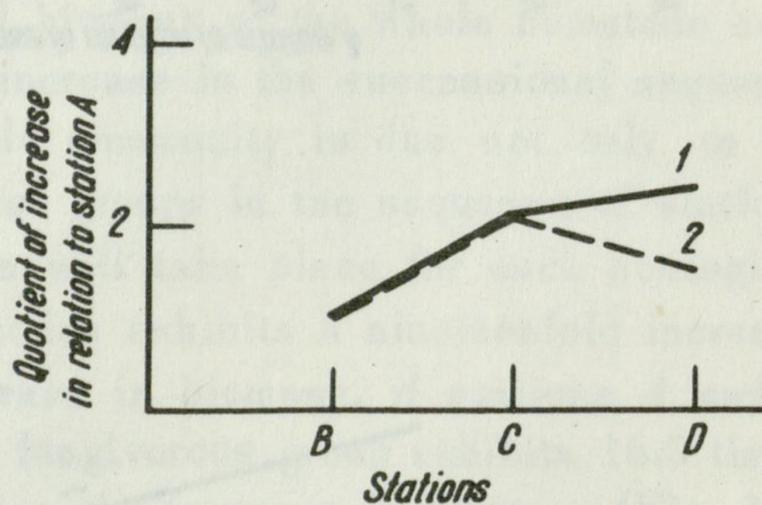


Fig. 14. Increase in numbers and biomass of omnivorous group on stations *B*, *C* and *D* in relation to station *A*
1 - numbers, 2 - biomass

weight of individuals in the order of successional sequence of stations occurs more or less regularly but not with uniform intensity in each ecological group (Fig. 16 and 17). Thus on stations with more advanced plant succession, that

Percentage of juveniles in relation to all nematodes calculated on basis of 6 samples taken jointly

Tab. VI

Working station	A	B	C	D
Microbivorous	88	80	80	83
Fungivorous	78	77	78	82
Parasites of higher plants	49	68	72	55
Omnivorous	60	69	66	80
Whole community	70	76	75	75

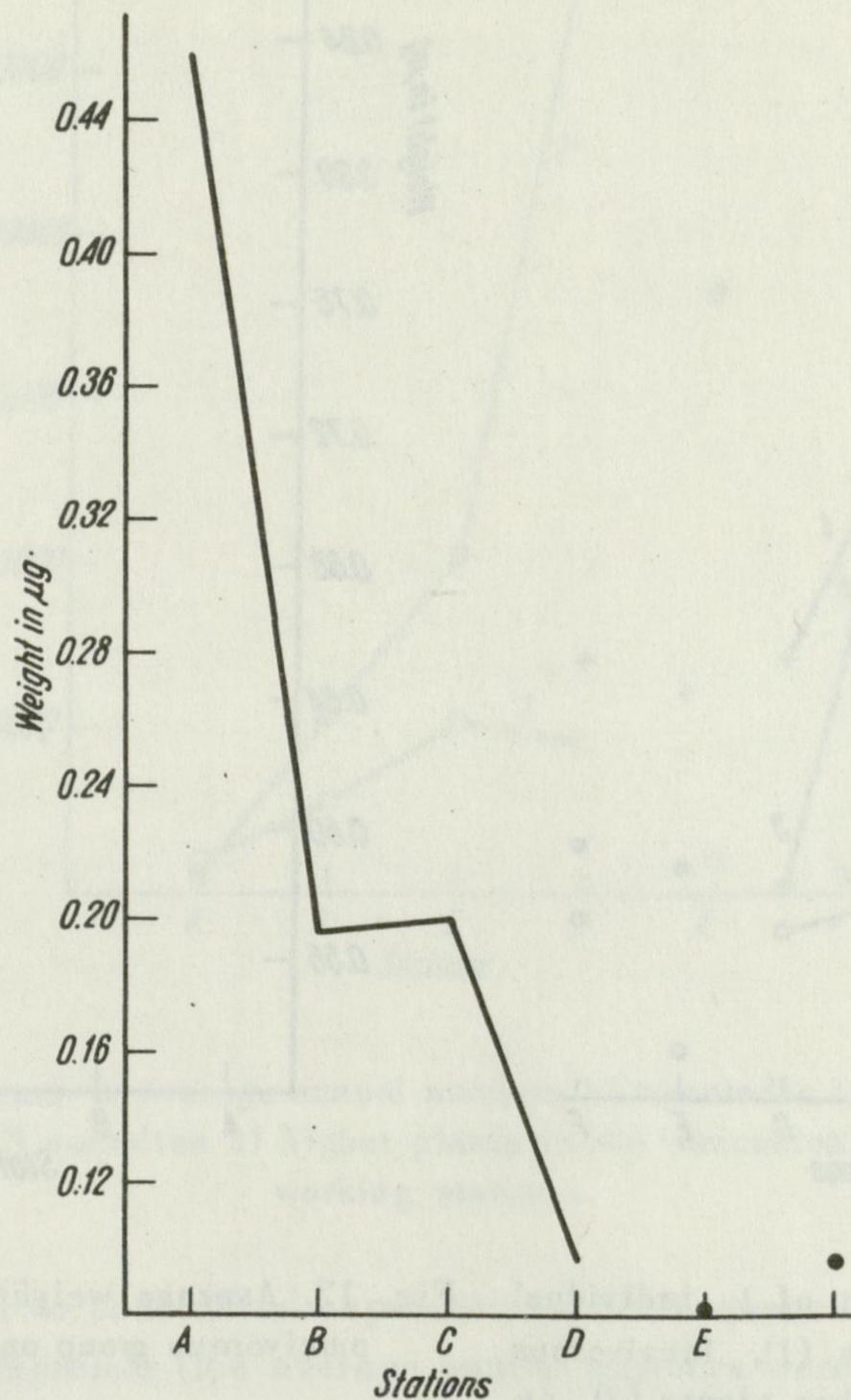


Fig. 15. Average weight of 1 individual in whole nematode community in the successional sequence of dune working stations (stations A – D) and in *Potentillo albae-Quercetum* (station E) and *Cladonio-Pinetum* (station F)

is, on “older” dunes in the afforested dune habitat it is on an average the small forms which predominate as compared with the “younger” dunes.

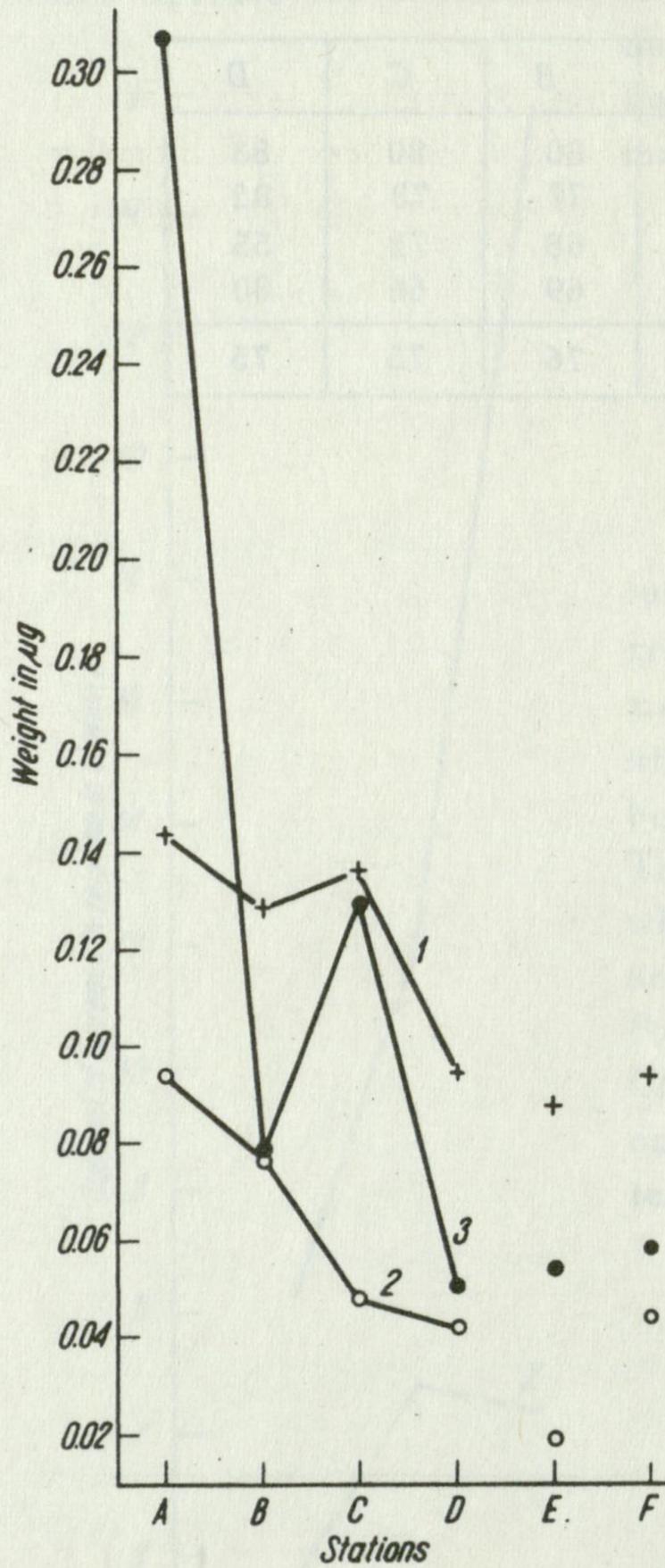


Fig. 16. Average weight of 1 individual from group: microbivorous (1), fungivorous (2) and parasites of higher plants (3) on working stations

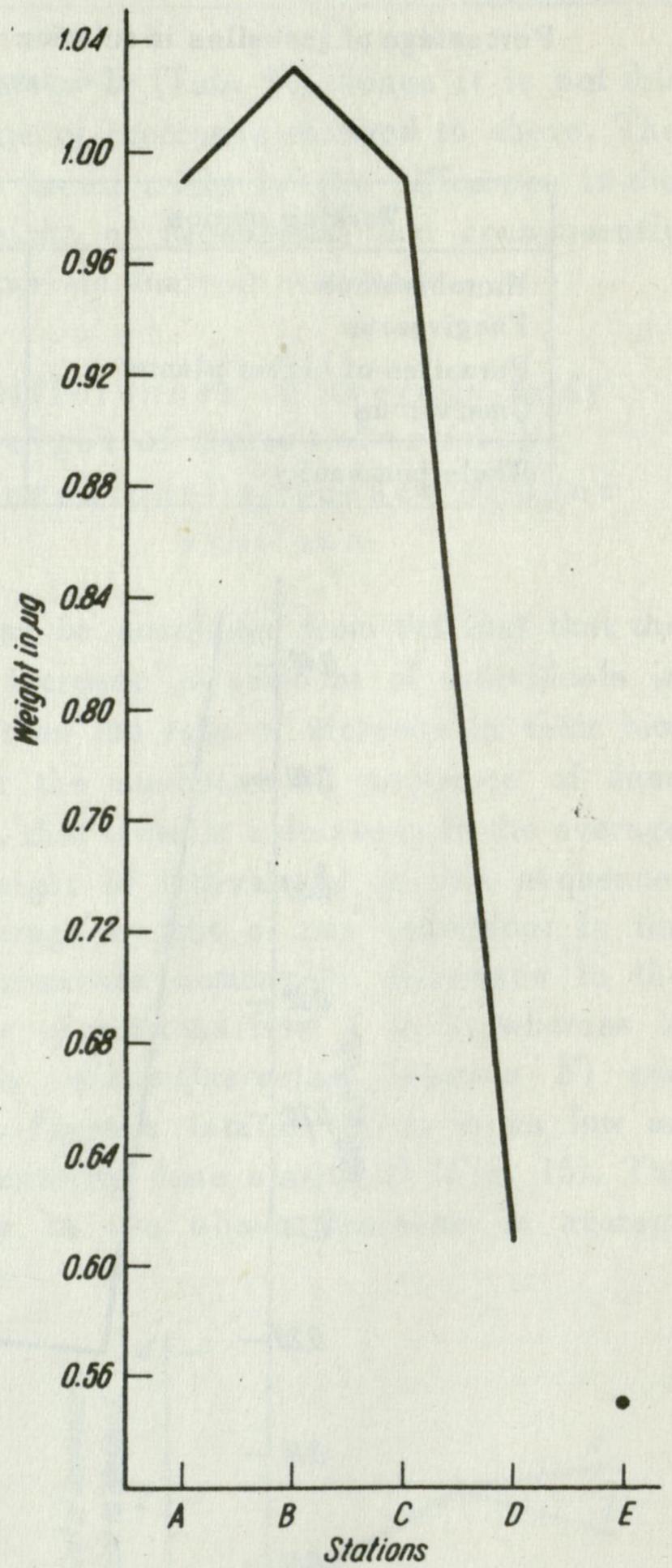


Fig. 17. Average weight of 1 individual from omnivorous group on working stations

5. Rate of increasing numbers and biomass of obligatory and facultative parasites in the successional sequence of dune stations

The group of nematodes feeding at the expense of higher plants has so far been treated as a whole, but the rate of increase in numbers and biomass of facultative parasites of plants and obligatory parasites (mainly migrating

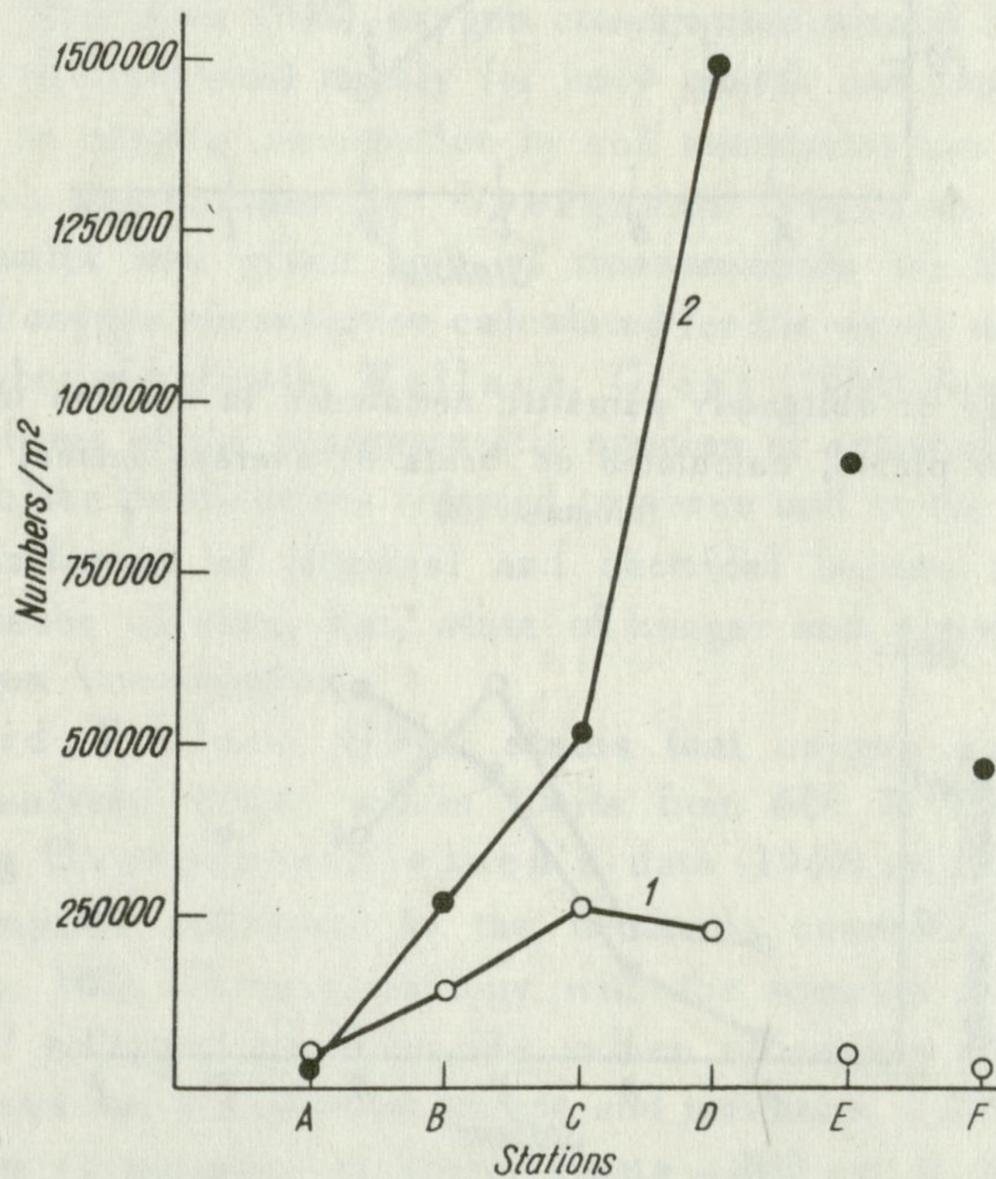


Fig. 18. Rate of increase in average annual numbers of nematodes from group: obligatory (1) and facultative (2) parasites of higher plants in the successional sequence of dune working stations

root parasites) will be considered separately in the sequence of stations from *A* to *D*. This rate of increase (the average annual numbers were used for purposes of comparison) in facultative parasites of plants is far more rapid than in obligatory parasites of plants (Fig. 18). Consequently the percentage of the numbers of obligatory parasites in relation to the whole group of parasites of higher plants markedly decreased in the successional sequence of dune stations (Fig. 19). The percentage of the biomass of obligatory parasites of plants in relation to the whole group of parasites of higher plants also distinctly decreased in the sequence of dune stations (Fig. 19), although increases in biomass took place not only among nematodes in the facultative groups,

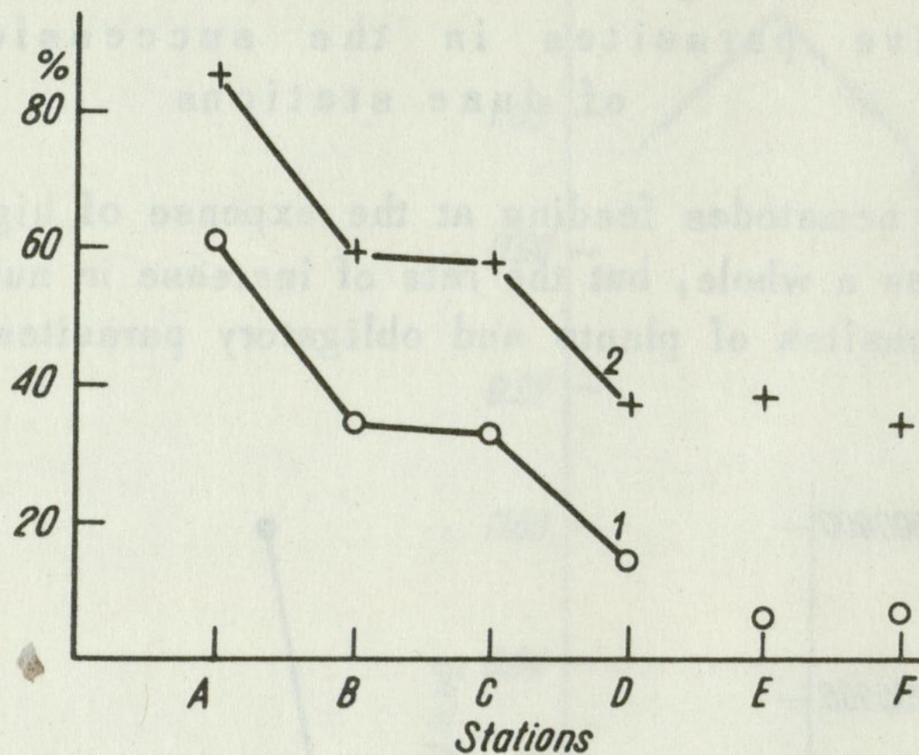


Fig. 19. Percentage of obligatory parasitic nematodes in relation to whole group of parasites of higher plants, calculated on basis of average annual numbers (1) and biomass (2)

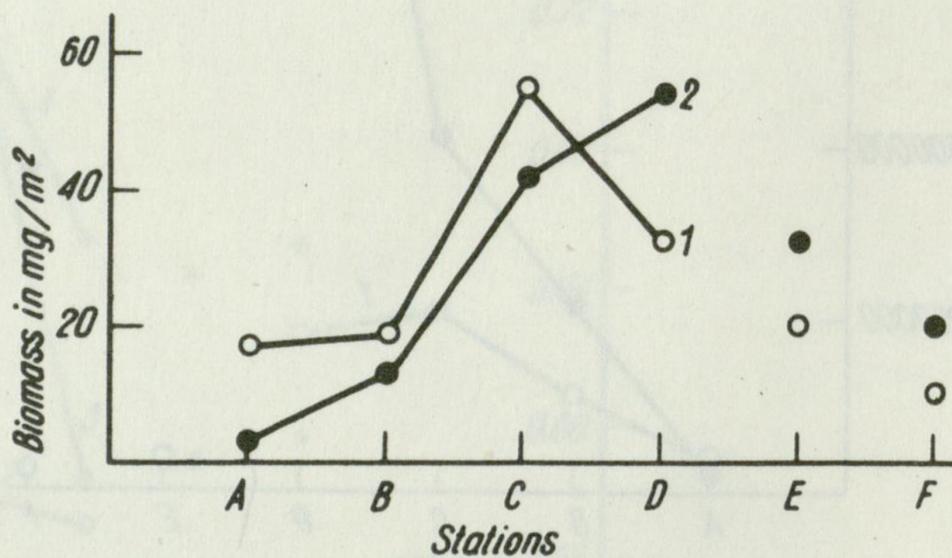


Fig. 20. Rate of increase in average annual biomass of nematodes from group: obligatory (1) and facultative (2) parasites of higher plants in the successional sequence of dune working stations

but also in the group of obligatory parasites of plants (Fig. 20). Data for stations *E* and *F* are contrasted in diagram form (Fig. 18–20).

The facts discussed above form evidence that the group of obligatory parasites of plants does not take on the character of domination as the vegetation cover becomes more luxuriant and the habitat more complex. The numbers of this group increased in accordance with the habitat parameters discussed, but decidedly more weakly than in the case of other, nematode non-obligatory parasites of plants.

VI. CALCULATED RESPIRATORY METABOLISM IN THE NEMATODE COMMUNITY

Overgaard Nielsen (1949) considers that the amount of food consumed by nematodes is in proportion to respiratory metabolism. Information on oxygen consumption may be useful primarily in estimating the importance of nematodes in organic processing of the soil. As resting and activity metabolism differs only slightly in aquatic and semi-aquatic animals (Brandt 1960a), and this has been proved for nematodes under experimental conditions (Overgaard Nielsen 1949), oxygen consumption should form the expression of the amount of food used mainly for body growth and reproduction.

Literature on oxygen consumption by soil nematodes has so far been based chiefly on two publications by Overgaard Nielsen (1949, 1961), in which the results are given both of measurements for 24 species of soil nematodes and oxygen consumption calculated for the whole nematode community in a large number of habitats. Wallace, Greet (1964) determined the oxygen consumption of one of the phytoparasitic species of nematode – *Tylenchorhynchus icarus*. In the publications referred to above and in the study by Brandt (1960b) the influence of physical and chemical factors is discussed, and also the influence of size, age, state of hunger and activity of nematodes on their oxygen consumption.

Overgaard Nielsen (1949) states that oxygen consumption by the species he analysed comes within limits from 600 to 1500 cm³ O₂/kg/hour at 16°C. Using Overgaard Nielsen's data (1949) as a basis I calculated oxygen consumption consumed by the nematode community on the stations analysed (Tab. VII). Through analogy with the species investigated by the above author I selected the following values of oxygen consumption: 1) for the microbivorous and fungivorous groups and predators – 1000 cm³ O₂/kg/hour, 2) for the group of parasites of higher plants – 800 cm³ O₂/kg/hour, 3) for the omnivorous group – 700 cm³ O₂/kg/hour, and 4) for the group with unknown food preferences – 1500 cm³ O₂/kg/hour.

Calculation of oxygen consumption was made separately for the growing season (from April to October) and separately as total annual consumption. Consumption during the growing season was calculated on the basis of samples taken five times during this period (data for June and August were interpolated from the data already possessed). Consumption during the remainder of the year (November-March) was based on data obtained for February. It must be remembered that calculated oxygen consumption for nematodes on the study stations is burdened with the following inaccuracies:

a) It is based on consumption determined for imaginal forms, whereas it is known (Overgaard Nielsen 1949) that juveniles are distinguished by more intensive respiration. Juvenile forms predominated in the habitat examined.

Calculated oxygen consumption (at 16°C) during growing season April-October (1)* and during whole year (2)** expressed in m³ O₂/ha

Tab. VII

Working stations Groups	A		B		C		D		E		F	
	1)	2)	1)	2)	1)	2)	1)	2)	1)	2)	1)	2)
Microbivorous	0.72	2.69	5.19	8.94	10.89	16.40	13.46	24.98	6.52	11.59	4.57	6.76
Fungivorous	0.67	1.05	1.28	2.45	1.64	2.99	4.11	6.99	1.90	2.34	1.08	1.88
Parasites of higher plants	0.87	1.09	1.49	1.86	4.47	5.89	3.85	5.97	2.11	3.31	1.34	1.42
Omnivorous	6.42	7.41	6.63	6.88	13.20	14.44	9.04	9.84	3.49	6.05	2.36	2.36
Predators	0	0	1.11	1.22	2.11	3.02	2.16	2.16	1.75	5.72	0	0
Food unknown	0.10	0.10	0.21	0.24	0.51	0.66	0.72	1.01	0.72	1.05	0.10	0.14
Whole community	8.78	12.34	15.91	21.59	32.82	43.40	33.34	50.95	16.49	30.06	9.45	12.56

* Consumption calculated for sum total of 5136 hours.

** Consumption calculated for sum total of 8784 hours.

b) Correction for temperature was not introduced. The measurements made by Overgard Nielsen (1949) refer to a temperature of 16°C. The effect of temperature on intensity of respiration is, according to his studies on one species of nematode, a very important factor. In the study habitat investigations were made of nematodes to depth of 25 cm and temperature varied in different layers of the soil. On account of the nematodes' capacity for vertical migration (daily and seasonal) in the direction of more favourable conditions the situation becomes even more complicated under natural conditions. The winter frost and summer drought periods require special studies on this point.

c) The possible period of anabiosis, which almost certainly occurs under the conditions characteristic of the species, was not taken into consideration. The conditions under which it occurs in the majority of free-living species were not examined. Wallace (1963) states that the low range of temperatures at which the majority of phytoparasitic nematodes become inactive is 5–15°C; the range of optimal temperatures is 15–30°C and range of high temperatures rendering nematodes inactive is 30–40°C. Many of the data on minimal, optimal

and maximal temperatures for assessing the activity of a very large number of soil and plant species of nematodes were collected by Dao (1970).

d) The methods used for extracting nematodes from soil are still far from perfect. The effectiveness of the extraction method used in this study is evaluated as about 80% of all soil nematodes (Szczygieł 1963), hence calculated consumption would be underestimated.

e) Transposition of measurements made under experimental conditions to natural conditions is always burdened with error.

The above remarks, and also the fact that approximate values for oxygen consumption by the species examined were accepted, should not, however, prove a hindrance to assessing the order of oxygen consumption value for the nematode community examined, particularly as literature on this subject is still very scanty.

The data given in table VII show that annual oxygen consumption by the nematode community was more than four times higher on the dune with 1.58% humus content and 48% plant cover (station *D*) in comparison with consumption by nematods from the dune with 0,24% humus content and 10% plant cover (station *A*). In the study nematode community two groups, omnivorous and microbivorous, were distinguished by maximum oxygen consumption and the remaining group by far lower consumption (Tab. VII). It is characteristic here that as succession advanced on the dunes (from station *A* to *D*) the importance of the microbivorous grup increased in respect of the amount of oxygen consumed. The omnivorous group did not exhibit such considerable increases in oxygen consumption as the microbivorous group, and even on the extreme station (*D*) a tendency to decreases could be discerned. The importance of the groups of parasites of higher plants and the fungivorous group increased in the successional sequence of stations when the amount of oxygen consumed is taken into consideration.

In studies on animals' food chains it is most convenient to present metabolism in units of energy. This was done in respect of the nematode community studied, using the following premises:

1) the ratio of proteins to fats and to carbohydrates in the nematodes' diet is 2 : 1 : 1 (after Overgaard Nielsen 1949),

2) 1 l of oxygen used in metabolism of proteins corresponds to 4.5 kcal, of fat – 4.7 kcal, of carbohydrates – 5 kcal (Prosser, Brown 1962) hence:

$$2 \times 4.5 \text{ kcal} + 4.7 \text{ kcal} + 5 \text{ kcal} = 18.7 \text{ kcal}$$

$$18.7 \text{ kcal} : 4 = 4.6 \text{ kcal}$$

therefore each litre of oxygen corresponds to 4.6 kcal. Metabolism of the whole soil nematode community in the study habitat during the growing season: April – October and for the whole year is given in table VIII.

Metabolism of the whole community of soil nematodes (at 16°C)
during growing season April-October 1)* and whole year 2)**

Tab. VIII

Working stations	A	B	C	D	E	F
1) kcal/ha period April-October	40 388	73 186	150 972	153 364	75 854	43 470
2) kcal/ha/year	56 764	99 314	199 640	234 370	138 276	57 776

* metabolism calculated for sum total of 5136 hours.

** metabolism calculated for sum total of 8784 hours.

The soil nematode community is not homogeneous in respect of trophic structure. The group of plant parasites may be considered as consumers of the first order. In the study habitat this group of nematodes per area of 1 ha consumes during the course of the year plant food at least with an energy value from 5014 to 27 462 kcal on afforested dunes, 15 226 kcal in *Potentillo albae-Quercetum* and 6 532 kcal in *Cladonio-Pinetum*. The full importance of this group is, however, only evident when the pathogenic activity of these nematodes resulting in injury to plant tissue, inhibition of growth etc. is taken into consideration.

The microbivorous and fungivorous groups can be considered as consumers of second order. The former group, per area of 1 ha consumes during the course of a year microorganisms with an energy value from 12 374 to 114 908 kcal on afforested dunes, 53 314 kcal in *Potentillo albae-Quercetum* and 31 096 kcal in *Cladonio-Pinetum*. For the fungivorous group these values are respectively from 4 830 to 32 154 kcal on afforested dunes, 10 764 kcal in *Potentillo albae-Quercetum* and 8 648 kcal in *Cladonio-Pinetum*.

The group of predators per area of 1 ha, as consumers of at least second order, consume animal food corresponding to an energy value from 5 612 to 13 892 kcal on afforested dunes and 26 312 kcal in *Potentillo albae-Quercetum* (this group is of no importance at all in *Cladonio-Pinetum*).

The omnivorous group contains representatives of consumers of several orders. The energy value of the food they consume, whether plant or animal, corresponds during the year to an energy value of 34 086 to 66 424 kcal on afforested dunes, 27 830 kcal in *Potentillo albae-Quercetum* and 10 856 kcal in *Cladonio-Pinetum*.

Determination of the variations in numbers of nematodes does not fully convey the importance of this group of animals in the habitat. It is also necessary to know both the biomass and metabolism of different trophic groups in order to assess their role in the food chain. The results present here indicate that seasonal dynamics in biomass are not always in proportion to dynamics

of numbers, e.g. in the group of plant parasites and the fungivorous group, although these two values are proportional in the microbivorous and omnivorous group. In addition the considerable differences in the body weight of individuals in different trophic groups result in the biomass of a less numerous group frequently exceeding the biomass of a far more numerous trophic group. The data given above on the metabolism of different trophic groups characterizes nematodes as consumers. In order fully to evaluate the role of nematodes in the food chain it is essential to determine their production, which in the case of nematodes is still attended by great difficulty.

VII. SUMMARY OF RESULTS

The following findings and conclusions were reached as the result of quantitative analysis of a nematode community on the afforested dunes of the Kampinos Forest:

1. On an average from 0.5 to 7 million soil nematodes per 1 m² of area were found to occur during the course of the year on the afforested dunes, while their biomass was from 0.2 to 0.7 g/m². In the mixed forest (*Potentillo albae-Quercetum*) this figure was 5 million nematodes per 1 m² (0.5 g/m²) and in dry pine forest (*Cladonio-Pinetum*) correspondingly 2 million per 1 m² (0.2 g/m²).

2. The following groups were most numerous represented in the nematode community in the following order: microbivorous, fungivorous and parasites of higher plants, but in respect of biomass the omnivorous and microbivorous groups predominated.

3. Seasonal variations in numbers and biomass in the nematode community of the afforested dunes was characterized by two main peaks: in spring and autumn, and two decreases: in summer and winter. There is some suggestion that the majority of the nematodes overwintered as juveniles, while a large part of the imagines existing in autumn died during the late autumn or winter period.

4. It can be concluded from the course taken by seasonal dynamics of ecological (trophic) groups that:

a) the microbivorous group, exhibiting high numbers during the peak periods, maintained a relatively high level of numbers and biomass during the winter,

b) the fungivorous group and parasites of higher plants were characterized by maximum level of numbers in spring,

c) during the winter there was considerable reduction in the numbers of nematodes from the group of parasites of higher plants, and fungivorous and omnivorous groups.

5. The influence of the plant succession on the afforested dunes (from the almost bare dune to the afforested one) on the nematode community is characterized by:

a) increase in numbers and biomass of the community, and increase in the amount of oxygen consumed as succession progresses,

b) increase in the percentage (of biomass and numbers) of the microbivorous group and decrease in the percentage of the omnivorous group,

c) non-uniform rate of increase in numbers and biomass in the successional sequence. Increase in numbers was far more rapid than increase in biomass in all the ecological groups,

d) decrease in the average body weight of individuals in the successional sequence, – resulting in forms on the average smaller predominating on the “older” dunes in comparison with the “younger” dunes,

e) more rapid rate of increase in the numbers of facultative parasites of plants in comparison with obligatory parasites. Consequently the percentage (of numbers and biomass) of obligatory parasites decreased in the successional sequence. Therefore the group of obligatory of plants fails to take on the characters of domination as the plant cover becomes more luxuriant and the habitat more complex,

f) almost four times higher annual oxygen consumption by the nematode community inhabiting the dune with 1.58% humus contents and 48% plant cover in comparison with nematodes from the dune with 0.24% humus content and 10% plant cover.

6. The calculated respiratory metabolism of the nematode community was expressed by oxygen consumption in amounts from approx. 9 to 33 m³/ha during the growing season, or from 12 to 51 m³/ha during the year on afforested dunes, and correspondingly 16 m³/ha and 30 m³/ha in *Potentillo albae-Quercetum* and 9 m³/ha and 13 m³/ha in *Cladonio-Pinetum*. These values can be expressed in units of energy, taking 4 600 kcal for each cubic metre.

7. In the nematode community analysed two groups: omnivorous and microbivorous – were distinguished by maximum oxygen consumption, far higher than in the remaining groups.

I am indebted to Professor dr. H. Sandner for his help during the course of this study.

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NICIENIE WYDM PUSZCZY KAMPINOWSKIEJ.

II. STRUKTURA ZGRUPOWANIA W OPARCIU O LICZEBNOŚĆ OSOBNIKÓW, STAN BIOMASY I METABOLIZM ODDECHOWY

Streszczenie

Przeprowadzono analizę ilościową zgrupowania nicieni wydm zalesionych Puszczy Kampinoskiej z uwzględnieniem grup troficznych nicieni. Analizy tej dokonano w sukcesyjnym szeregu stanowisk wydmowych, począwszy od wydmy bardzo skąpo pokrytej roślinnością (10% pokrycia przez rośliny naczyniowe) i o niskiej zawartości próchnicy w glebie (0,24%) do wydmy zadrzewionej 20-letnim drzewostanem, o 48% stopniu pokrycia przez rośliny naczyniowe i zawartości próchnicy glebowej 1,58% oraz porównawczo w borze mieszanym (*Potentillo albae-Quercetum*) i borze suchym (*Cladonio-Pinetum*). Opis stanowisk i metodyki podano w pierwszej części pracy, która dotyczyła analizy struktury gatunkowej (Wasilewska 1970). Omówiono sposób zaszeregowania gatunków do grup troficznych (Tab. II) oraz podano krytyczny wybór metody wyznaczania ciężaru ciała nicieni (Tab. III i IV).

W niniejszym opracowaniu analizowano gęstość zasiedlenia nicieni w badanym środowisku zarówno na podstawie liczebności jak i stanu ich biomasy. Porównano gęstość zasiedlenia nicieni i stanu ich biomasy w środowisku wydm zalesionych z innymi typami habitatów jak lasy, pustynie, tereny trawiaste i uprawne (Tab. I). Przeanalizowano dynamikę sezonową liczebności i stanu biomasy zarówno całego zgrupowania, jak i poszczególnych grup ekologicznych (1 – bakteriofagi, 2 – mykofagi, 3 – pasożyty roślin wyższych, 4 – wszystkożerne i 5 – drapieżce). Ustalono wpływ sukcesji roślinnej na wydmach zalesionych na stosunki ilościowe (liczebność osobników, stan biomasy) pomiędzy grupami troficznymi nicieni. Stosunki te dotyczyły zarówno udziału grup troficznych, tempa narastania liczby osobników i biomasy, jak i różnic w przeciętnym ciężarze ciała nicieni w szeregu sukcesyjnym stanowisk wydmowych. Przeanalizowano dodatkowo znaczenie obligatoryjnych pasożytów roślin w miarę komplikowania się analizowanego środowiska naturalnego. W końcu przeprowadzono kalkulację metabolizmu oddechowego całego zgrupowania i poszczególnych grup troficznych

nicieni w oparciu o pomiary konsumpcji tlenu przez nicienie dokonane przez Overgaard Nielsena (1949). Wysznięto następnjące stwierdzenia i wnioski.

1. Na wydmach zalesionych stwierdzono występowanie średnio w roku od 0,5 do 7 milionów nicieni glebowych na 1 m² powierzchni, zaś biomasa ich wynosiła od 0,2 do 0,7 g/m². W barze mieszanym (*Potentillo albae-Quercetum*) stwierdzono występowanie 5 milionów nicieni na 1 m² (0,5 g/m²), zaś w borze suchym (*Cladonio-Pinetum*) odpowiednio 2 miliony na 1 m² (0,2 g/m²) (Tab. V).

2. W zgrupowaniu nicieni najliczniej reprezentowane były kolejno grupy: bakteriofagi, mykofagi i pasożyty roślin wyższych, pod względem jednak biomasy przodowały: grupa wszystkożernych i grupa bakteriofagów (Fig. 9).

3. Sezonowe zmiany liczebności i biomasy zgrupowania nicieni wydm zalesionych charakteryzowały się dwoma głównymi szczytami: wiosennym i jesiennym oraz dwoma spadkami: letnim i zimowym (Fig. 1). Istnieją pewne sugestie, że większość nicieni zimowała w stadium młodocianym, zaś znaczna ilość egzystujących jesienią osobników dorosłych ginęła w okresie zimowym lub późnojesiennym (Fig. 1 i 2).

4. Z przebiegu sezonowej dynamiki grup ekologicznych (troficznych) nicieni można było wnioskować o tym, że:

a) grupa bakteriofagów, wykazując wysoką liczebność w okresie szczytów, zachowała stosunkowo wysoki poziom liczebności i biomasy w okresie zimy (Fig. 3),

b) grupa mykofagów i pasożytów roślin wyższych charakteryzowała się najwyższym poziomem liczebności w okresie wiosennym (Fig. 4 i 5),

c) w okresie zimy następowała znaczna redukcja liczebności nicieni z grupy pasożytów roślin wyższych, grupy mykofagów i grupy wszystkożernych (Fig. 4, 5 i 7).

5. Wpływ sukcesji roślinnej na wydmach zalesionych (od wydmy prawie nagiej do zadrzewionej) na zgrupowanie nicieni charakteryzował się:

a) wzrostem liczebności i biomasy zgrupowania, jak i wzrostem ilości konsumowanego tlenu w miarę postępowania sukcesji (Tab. V i VII),

b) wzrostem udziału liczebności i biomasy grupy bakteriofagów i spadkiem udziału grupy wszystkożernych (Fig. 9),

c) niejednakowym tempem narastania liczebności i biomasy w szeregu sukcesyjnym stanowisk (Fig. 10). Przyrost liczebności był zawsze szybszy niż przyrost biomasy we wszystkich grupach ekologicznych (Fig. 11, 12, 13 i 14),

d) zmniejszaniem się średniego ciężaru ciała osobników w szeregu sukcesyjnym – zatem, na wydmach „starszych” przeważały formy, przeciętnie biorąc, drobniejsze, w porównaniu z wydmami „młodszyymi” (Fig. 15, 16, 17),

e) szybszym tempem narastania liczebności fakultatywnych pasożytów roślin w porównaniu z obligatoryjnymi. W związku z tym udział (liczebności i biomasy) pasożytów obligatoryjnych malał w szeregu sukcesyjnym. Zatem w miarę wzbogacania się szaty roślinnej i komplikowania się środowiska grupa obligatoryjnych pasożytów roślin nie nabierała cech dominowania (Fig. 18, 19 i 20),

f) przeszło czterokrotnie wyższą roczną konsumpcję tlenu przez zgrupowanie nicieni zasiedlających wydmy o zawartości próchnicy 1,58% i pokryciu roślinnością naczyniową 48% w porównaniu z nicieniami z wydmy o zawartości próchnicy 0,24% i pokryciu 10% (Tab. VII).

6. Wykalkulowany metabolizm oddechowy zgrupowania nicieni wyrażał się konsumpcją tlenu w ilości od 9 do 33 m³/ha w okresie wegetacyjnym lub od 12 do 51 m³/ha w okresie roku na wydmach zalesionych, odpowiednio 16 m³/ha i 30 m³/ha w borze mieszanym (*Potentillo albae-Quercetum*) i 9 m³/ha i 13 m³/ha w borze suchym (*Cladonio-Pinetum*) (Tab. VII). Wartości te można wyrazić w jednostkach energetycznych, przyjmując za każdy metr sześcienny tlenu 4 600 kcal (Tab. VIII).

7. W analizowanym zgrupowaniu nicieni dwie grupy: wszystkożerne i bakteriofagi odznaczały się największą konsumpcją tlenu, znacznie wyższą niż grupy pozostałe (Tab. VII).

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