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AN ANALYSIS OF *COLLEMBOLA* COMMUNITIES IN DIFFERENT PINE FOREST ENVIRONMENTS*

ABSTRACT: Studies of the relationship the density of *Collembola* in a pine forest and the soil moisture of the habitat have shown: (1) a maximum *Collembola* density at average values of the plot moisture gradient, (2) a higher level of density during full growing season, (3) a higher maximum density during the warm season (June-September) on moister plots. Competitive relations were manifested by the occurrence of compensatory changes in the density of the selected groups of oligo- and polyvalent species under different habitat conditions. The density of oligovalent species appeared to depend to a considerable extent on moisture, that of polyvalent species — on the density of the oligovalent species. Among species with similar ecological reactions a tendency was found to avoid occurring together in the same territory.

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1. INTRODUCTION

The *Collembola* provide rather a specific object for ecological studies. Nearly all the more abundant species of the temperate zone belong to eurytopic forms (occurring in all terrestrial environments), their distribution range often being cosmopolitan (Stach 1947, 1949a, 1949b, 1951, 1954, 1956, 1957, 1960, 1963, Kühnelt 1950). The continuous reproductive capability [some of the species are capable of parthenogenetic reproduction — Petersen (1971)], and the activity throughout the year make it possible for the population to grow in numbers fast and in almost any period of the year, which has been confirmed by the results of studies of the variation in population density carried out in various environments (Weis-Fogh 1948, Sheals 1957, Poole 1961, Milne 1962, M. Kaczmarek 1963, Choudhuri and Roy 1967, Vannier 1970 and many others). These studies have revealed that in most species both the variation in numbers with time, and the differences in distribution within individual biotopes are considerable and difficult to explain by the phenology of the species, or by soil properties and vegetation. For the same species different annual cycles are often found, and the species attain various population density levels in very similar environments, and similar cycles and population density levels in environments essentially different. It follows from this that the factors determining the density of most *Collembola* species are factors whose action is very common, affecting various biotopes. Among the environmental factors of this type of particular importance are moisture, temperature, food resources in the habitat, and possibly competitive relations.

There is a fairly close relationship between *Collembola* population density and soil moisture (Hammer 1944, Strenzke 1949, Margowski and Prusinkiewicz 1955, Stevanovič 1956, Vannier 1971), the degree of hygrophilia of the species being the best criterion for their ecological classification (Agrell 1941, Gisin 1957).

The species appear to differ to some extent in respect of their response to variations in temperature (Agrell 1941, Edwards and Lofty 1971). A clearly differentiating effect of temperature could be seen during the analysis of the mobility of the epigeic *Collembola* fauna (M. Kaczmarek 1960, Joosse 1971). However, the problem of a direct effect of temperature on the density of *Collembola*, except periods of extremely low temperature when reproduction stops, seems to be objectionable, the more so as peak densities of *Collembola* occur in periods of highly variable temperature (Glasgow 1939, Schaller 1949, Vander Drift 1951, Dowdy 1965, McMillan 1969).

Finally, on the basis of the yearly cycle of *Collembola* density in moist habitats a presumption has been put forward that under these conditions the level of *Collembola* density and its annual variations may depend on the food factor (Weis-Fogh 1948, Strenzke 1949, Kühnelt 1950, M. Kaczmarek 1963).

The main purpose of the present study was to compare the reactions of the most abundant *Collembola* species to variations in soil moisture in a pine forest. In order to be able to determine the effect of habitat moisture as univocally as possible a method of analysing the results was used in which variations in numbers of the selected insect species were compared in two aspects — over a yearly cycle and over an environmental gradient. The autecological data thus

obtained provided a basis for the interpretation of the interspecific relations, and the analysis of the latter was another purpose of the study. To assess any possible competitive relations within the *Collembola* community under study annual variations in the percentage contribution, and the distribution of individual species were compared with their density and distribution expected on account of their habitat specialization.

2. STUDY AREA AND METHODS

The research was carried out in a large woodland area, a large tract of lowland pine forest (Łobodno Forest Inspectorate, Lemańsk Forest District). The soils found there are slightly podzolized soils with the eluvial horizon at a maximum depth of 20–35 cm (H a b e r 1957).

Five plots, each of about 0.5 ha and at a distance of about 2–3 km from one another, were selected. They were designated with the numerals I to V to form a gradient in ascending order of soil moisture (Tab. I).

Soil moisture was determined as a percentage difference between the dry weight and wet weight of soil after drying for 10 h at 105°C. As it was impossible, for technical reasons, to continue a regular checking of soil water content on all plots, measurements were made once only (in autumn when the precipitation rate was low). The basis used was the assumption of parallel soil moisture variations in different plots, as indicated by studies in other areas (P e r e l 1964, H. T r a c z y k and T. T r a c z y k 1965), and by unpublished data of the Department of Biocenology of the Institute of Ecology, Polish Academy of Sciences. Since these data are a kind of index data only, they were used solely for arranging the plots under study into a soil-moisture gradient.

The canopy-density ratio values in Table I represent the surface of tree-top projections on the forest floor, they thus indicate the degree of shading of the lower vegetation layers, and the soil, by the tree layer.

The data on precipitation, temperature and relative air humidity used in the paper have been obtained from the local Station of the Institute of Meteorology and Water Economics¹.

From each plot 50 randomly distributed samples (each core = 10 cm² and 10 cm in depth) were collected at a time [soil-sampler cf. M. K a c z m a r e k (1963)]. After dividing the sample into litter and soil-layers the fauna was extracted from them on the funnels of a simplified Tullgren's apparatus for three days at room temperature. This method of obtaining *Collembola* from soil samples is one of the most widely used methods (E d w a r d s and F l e t c h e r

Tab. I. Description of plots

Plot	Soil moisture (%)	Age of tree-stand (years)	Canopy density (complete = 1)
I	6.0	34	0.7
II	7.7	65	0.8
III	9.4	41	0.9
IV	10.7	69	0.7
V	13.4	55	0.8

¹For the elaboration of the material for the description of air humidity and total precipitation a unit of 10 days preceding the sample collecting was adopted. The reason for this was that the individual development of *Collembola* lasts about 30 days, and the first developmental stages are very small and may escape one's notice. Therefore the effect of environmental conditions on the emergence of individuals is probably noticeable after 10 days.

1971). The samples thus collected (a total of 2200) made it possible to determine the variations in population density throughout the season (Tab. II), the vertical distribution (litter-soil) of *Collembola*, as well as the distribution within individual plots. The sample-size used and the number of samples in a series conformed to the criteria required for the analysis of interspecific relations on the basis of species coincidence (T a r w i d 1960). For the determination of this coincidence F o r b e s' (1907) coefficient was used:

Tab. II. Number of samples taken during individual periods

Plot	Period											
	12-13 April	7-9 May	25-31 May	18-20 June	4-9 July	25 July	2-8 Aug.	20 Aug.	3-11 Sept.	13-21 Oct.	10-20 Nov.	12-19 Dec.
I			50		50		50		50	50	50	50
II		50	50	50	50	50	50	50	50	50	50	50
III			50		50		50		50	50	50	50
IV	50	50	50	50	50		50		50	50	50	
V	50	50	50	50	50		50		50	50	50	50

$$Sc_{AB} = \frac{n_{AB}}{n_p} \quad (1)$$

where $n_p = \frac{n_A \cdot n_B}{n}$, n_{AB} — the actual number of samples in which both species were encountered, n_p — the expected number of samples in which these species should occur together, assuming their independent occurrence in samples, n_A — number of samples with species A in the given sample series, n_B — number of samples with species B in this series, n — total number of samples in a series.

If the coefficient is greater than one, that is, if the number of samples in which the species occur together is greater than the expected number of simultaneous occurrences of these species under the given conditions, it means that the species tend to occur together in the samples. A coefficient value equal to one indicates that the territorial occurrence of the species is independent, their coincidence in the samples being a matter of chance. Finally, if the coefficient value is less than one, the species in question tend to occur in the samples separately.

This coefficient has been used in many ecological papers (F o r b e s 1907, D i c e 1945, W. K a c z m a r e k 1953, W a s i l e w s k i 1967). Its weak point is its being to a large extent affected by the frequency of the species compared, and on the other hand it is difficult to verify statistically (K a j a k 1957, T a r w i d 1960).

In order to evaluate the variation of this coefficient with a variable number of samples in a series, and variable species frequency the mean value of the coefficient and its error were analysed for series of 10, 20, and 50 samples taking into account four different frequency variants: when both species occur equally frequently (species A occurs in 0.8 samples of series and species B occurs also in 0.8 samples; species A occurs in 0.5 samples of series and species B occurs also in 0.5 samples), when both species occur rarely (species A occurs in 0.2 samples of series and species B occurs also in 0.2 samples), when one species is frequent and the

other rare (species A occurs in 0.7 samples of series but species B occurs in 0.2 samples). The values of the coincidence coefficient for all the cases enumerated were found for data obtained by using a modelling procedure based on random number tables. To illustrate the operation let us consider a case where the probability of species A appearing in a sample series equals 0.2, probability of samples with B = 0.7. Taking into account two independent sequences of k random numbers (k = number of samples per a series = 10), in the first sequence we assign value A to figures 0 and 1 (species A has occurred), and absence of A to the remainder of figures. In the second sequence we assign presence of species B to figures 2, 3, ..., 8 and absence of the species to the remainder of figures.

For each random sampling (25 up to 100 random samplings were made for each variant) the value of the coefficient of coincidence was calculated for species A and B. The summary of the mean values of the coefficient and their error (Tab. III) shows that the coefficient value is most different from unity with variants $P(A) = 0.2; P(B) = 0.2$ and $P(A) = 0.2; P(B) = 0.7$. With the size of the sample series being equal to 50, the coefficient values in the two extreme cases vary from 0.945 ± 0.20 to 1.39 ± 0.038 ; therefore, considering the magnitude of the error, one should assume that the coefficient values calculated from the material and greater than 1.427 indicate a real tendency of the species to coincide, whereas values less than 0.745 – a real tendency to occur separately.

Tab. III. Value of coincidence coefficient in the case of independent occurrence of species, based on modelling method

For explanation of the symbols see the text

Number of samples in a series	Variant			
	$P(A) = 0.2$ $P(B) = 0.2$	$P(A) = 0.5$ $P(B) = 0.5$	$P(A) = 0.2$ $P(B) = 0.7$	$P(A) = 0.8$ $P(B) = 0.8$
10	0.696 ± 0.24	0.98 ± 0.084	1.35 ± 0.061	0.997 ± 0.027
20	0.839 ± 0.23	1.04 ± 0.060	1.38 ± 0.055	0.998 ± 0.024
50	0.945 ± 0.20	1.03 ± 0.076	1.39 ± 0.038	0.997 ± 0.020

This has been taken into account in the paper where only coefficient values above 1.5 were considered to indicate territorial convergence, and values below 0.75 – divergence of occurrence.

In addition to the above-discussed coefficient of coincidence (Sc_{AB}) the author used the coefficient of similarity in ecological reactions (Sm_{AB}), introduced in order to compare the proportion of density variations of species A and B with time.

This proportion was determined by a specially elaborated formula which compares deviations of density from the mean value of density in either species of a pair of species studied, throughout the study period.

$$Sm_{AB} = n : \left[\bigwedge_{a_i > b_i} \sum_{i=1}^n \left(\frac{a_i}{\bar{a}} : \frac{b_i}{\bar{b}} \right) + \bigwedge_{b_i > a_i} \sum_{i=1}^n \left(\frac{b_i}{\bar{b}} : \frac{a_i}{\bar{a}} \right) \right] \quad (2)$$

Tab. IV. Species composition and occurrence (+) in individual plots

Species	Plot					Total number of individuals
	I	II	III	IV	V	
<i>Hypogastrura armata</i> (Nic.)		+				2
<i>Xenylla brevicauda</i> (Tullb.)	+	+	+	+		4
<i>Schoettella inermis</i> (Tullb.)	+	+	+	+	+	101
<i>Brachystomella parvula</i> (Schäff.)			+			1
<i>Willemia anophthalma</i> Börn.	+	+	+	+	+	311
<i>Friesea mirabilis</i> (Tullb.)					+	1
<i>Anurida pygmaea</i> Börn.	+	+	+	+	+	162
<i>Neanura muscorum</i> (Templ.)	+	+	+	+	+	32
<i>Onychiurus granulatus</i> Stach		+		+		8
<i>O. absoloni</i> (Börn.)	+	+		+	+	31
<i>O. sp.</i>				+	+	6
<i>Tullbergia krausbaueri</i> (Börn.)	+	+	+	+	+	187
<i>Folsomia quadrioculata</i> (Tullb.)	+	+	+	+	+	1062
<i>F. sp. sp.</i>				+	+	4
<i>Anurophorus laricis</i> Nic.	+	+	+	+	+	1275
<i>Isotomiella minor</i> (Schäff.)	+	+	+	+	+	1737
<i>Isotoma notabilis</i> Schäff.	+	+	+	+	+	1443
<i>I. sp.</i>		+			+	16
<i>Tomocerus flavescens</i> (Tullb.)	+	+	+	+	+	25
<i>Orchesella bifasciata</i> Nic.	+	+	+	+	+	284
<i>O. multifasciata</i> Scherb.	+		+	+	+	35
<i>O. flavescens</i> (Bourl.)		+	+	+		18
<i>Entomobrya corticalis</i> (Nic.)			+	+	+	10
<i>E. nivalis</i> (L.)	+	+	+	+	+	19
<i>E. multifasciata</i> (Tullb.)		+	+	+		8
<i>E. marginata</i> (Tullb.)	+		+			3
<i>Lepidocyrtus lanuginosus</i> (Gmel.)	+	+	+	+	+	706
<i>L. cyaneus</i> Tullb.					+	5
<i>L. violaceus</i> Lubb.			+		+	2
<i>Entomobryidae sp. sp. juv.</i>	+	+	+	+		73
<i>Megalothorax minimus</i> Will.	+	+		+	+	13
<i>Sminthurides violaceus</i> (Reut.)		+				10
<i>Sminthurinus niger</i> (Lubb.)	+	+	+	+	+	18
<i>Stenacidia violacea</i> (Reut.)	+		+		+	8
<i>Sminthurus viridis</i> (L.)		+				1
<i>Dicyrtoma fusca</i> (Luc.)		+				2
<i>Ptenothrix atra</i> (L.)		+				3
<i>Sminthuridae sp. sp. juv.</i>	+	+	+	+	+	44
Total number of individuals						7770
Total number of species	20	26	23	24	25	
wherefrom <i>Symphyleona</i>	3	6	2	2	3	

where: a_i, b_i – the density of species A and B at i -th point of time, n – number of time points, \bar{a}, \bar{b} – average density of species A and B for a point of time.

The value of the coefficient may vary from zero (when density variations are entirely opposite – a fully divergent ecological reaction of the species under study) to one (when there is a full similarity of density variations – an identical ecological reaction of the species under study).

3. COMMUNITY COMPOSITION

The species composition of the *Collembola* obtained from all the samples collected was in principle typical of the pine forests (Volz 1934, Agrell 1941, Jahn 1950, Böckemühl 1956). The number of species found in individual plots was very similar: for the suborder *Arthropleona* it varies between 17 and 22 (Tab. IV).

The increasing number of species from sample to sample makes one presume that the species composition of some of the plots in the material presented is not yet complete, and any differences in this respect may be a matter of chance (Tab. V).

Tab. V. Number of *Collembola* species of the suborder *Arthropleona* in consecutive samples

Plot	Number of consecutive samples										
	50	100	150	200	250	300	350	400	450	500	550
I	11	12	15	16	16	16	17				
II	5	9	10	12	18	19	19	20	20	20	20
III	11	13	17	18	21	21	21				
IV	10	13	15	15	16	18	20	22	22		
V	8	14	16	18	19	19	22	22	22	22	

The object of a detailed analysis in the present study was the most numerous species: *Isotomiella minor*, *Isotoma notabilis*, *Folsomia quadrioculata*, *Anurophorus laricis*, *Lepidocyrtus lanuginosus*, *Willemia anophthalma*, *Tullbergia krausbaueri*, *Anurida pygmaea*, *Orchesella bifasciata*. On each plot these species jointly represented about 90% of the community. Already in the first 100 samples all these species were found to occur in all the plots simultaneously. We are, therefore, dealing with the same *Collembola* community everywhere.

4. TOTAL DENSITY

4.1. Habitat optimum

The distribution of the annual average density of *Collembola* in the plots studied indicates highest densities in the medial intervals of the gradient considered (Fig. 1). Simultaneously, when comparing the average densities for different periods of the year, it is possible to notice some very characteristic shifting of the density peaks over the plot gradient under study (Fig. 2)². With the lowest air humidity (May, May-June) the peak density of *Collembola* occurred in

²The location of the peaks and the density differences found are well proved by the considerable regularity of the changes over the plot gradient under study: in all the cases analysed the density of *Collembola* decreased consistently, from the peak point down towards the extreme points of the gradient.

the moistest plot (V), and it moved steadily towards drier plots as the air humidity increased. Consequently, peak densities accompanied higher and higher air humidity: in plot IV (October), in plot III (August, September) and in plot II (July and November-December). Finally, in no period was the density of *Collembola* in plot I, the driest of all, higher than in the remainder of the plots.

This consistent convergence of density distribution in the plots and the relative air humidity indicates that under the conditions of the research humidity played the role of a factor determining the habitat optimum of the whole *Collembola* community, and that over the recorded course of the meteorological conditions the annual average optimum habitat moisture was in the middle interval of the habitat gradient considered: the moistest plots were too moist, the driest plot was too dry. The driest plot was entirely outside the optimum moisture of the community (throughout the year), as indicated by the fact that during none of the periods was highest density of *Collembola* found in it. Moreover, *Collembola* popula-

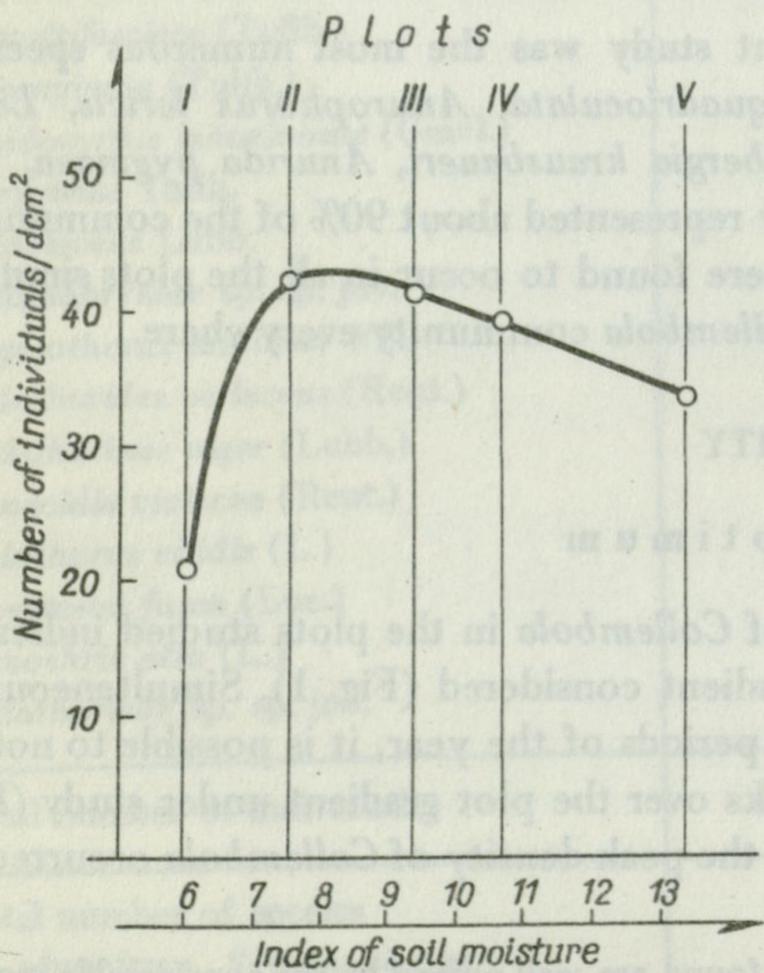


Fig. 1. Average annual density of *Collembola* in plots

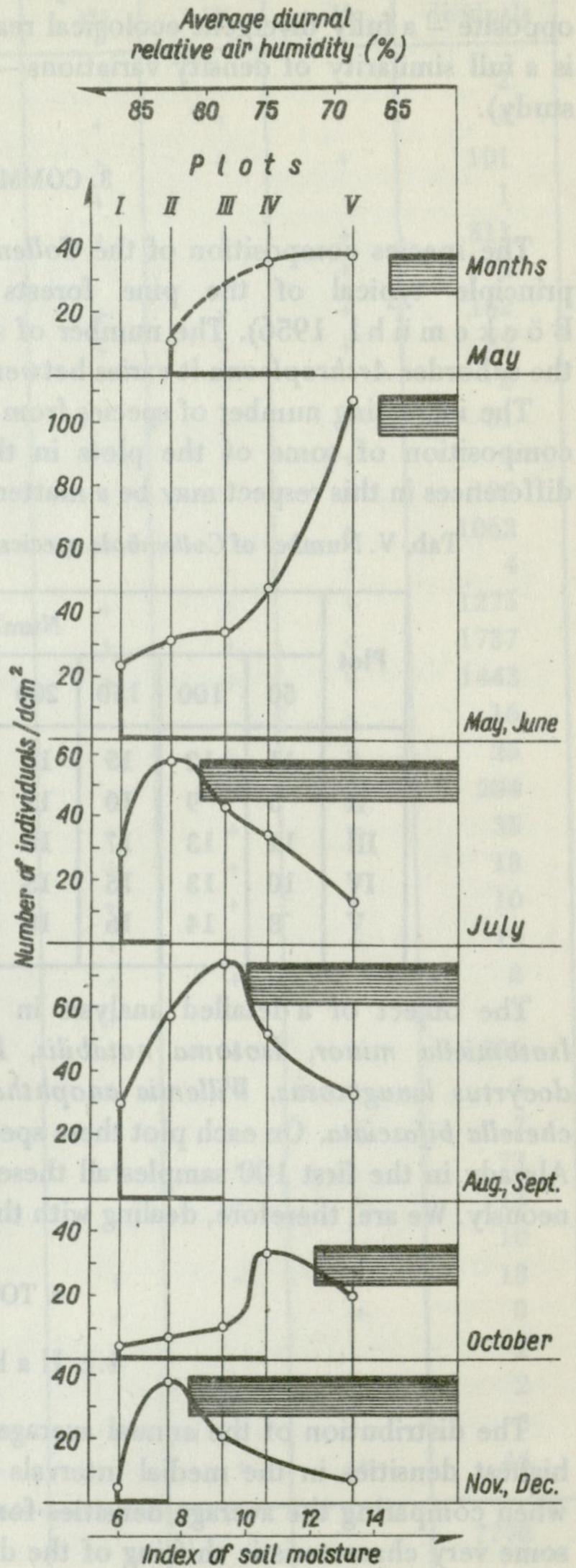


Fig. 2. Average density of *Collembola* in consecutive periods from May to December against the gradient of habitat moisture and the average diurnal relative air humidity over the ten-day period preceding the catches

tion density was nearly always lowest there except one significant case: in July when the relative air humidity was very high, and so was the precipitation rate, the lowest population density was recorded for plot V, the moistest of all. At that time the density of *Collembola* in plot I was about twice as high as that in plot V (Fig. 2). It may be stated, therefore, that in plot I, in general, pessimum conditions prevailed except for a period of an extremely high moisture when pessimum conditions moved to the moistest plot, i.e., plot V. Possibly, an additional factor affecting the density of *Collembola* in plot I was the young age of the tree stand [J a h n (1950) and M a r g o w s k i (1952) found that the density of *Collembola* increased with the age of the pine stands investigated by them]. However, the differences in density in the remainder of plots (II-V), in spite of the wide range of stand age (Tab. I), did not show any relationship to this factor.

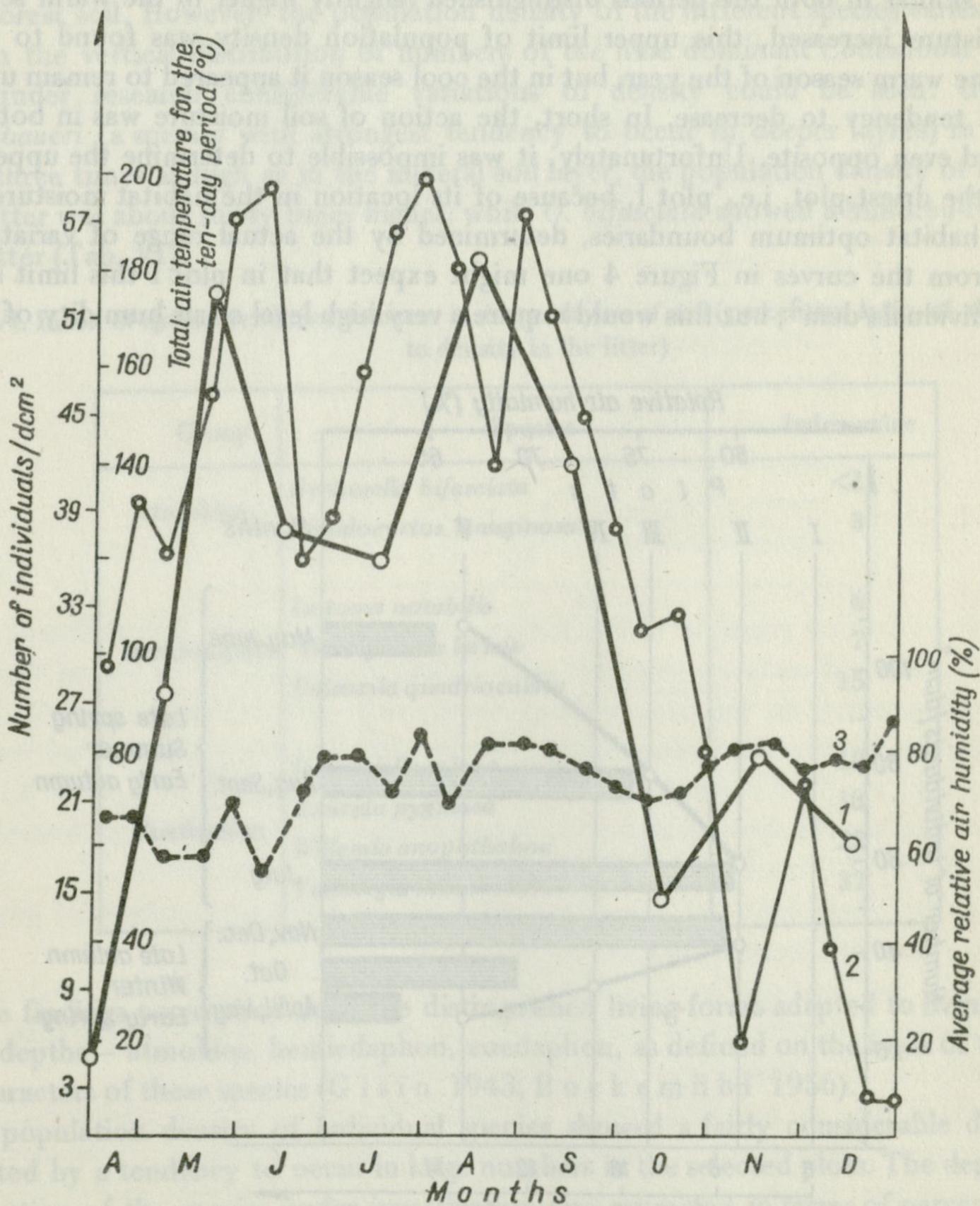


Fig. 3. Average monthly density of *Collembola* in the study area against the course of air temperature and its relative humidity

1 — density of *Collembola*, 2 — temperature, 3 — relative air humidity

4.2. Variation of density level with time

The course of seasonal variations of the average density of *Collembola* in the area under study did not show any clear picture of their relationship to temperature, or relative air humidity, although the overall level of density during the growing season was clearly higher than that recorded for the period between late autumn and early spring (Fig. 3). This lack of more noticeable differences was caused by the seasonal movement of the habitat optima, due to which the picture becomes blurred. By appropriately sorting the data we can see a characteristic difference in the reaction of *Collembola* to moisture variations in the above-named two periods (Fig. 4).

In plots with a low soil moisture the upper limit of numbers of *Collembola*, with an optimum interaction of air humidity and soil moisture (cf. habitat optimum Section 4.1), was found to be similar in both the periods distinguished (slightly higher in the warm season). As the soil moisture increased, this upper limit of population density was found to markedly increase in the warm season of the year, but in the cool season it appeared to remain unchanged with a slight tendency to decrease. In short, the action of soil moisture was in both periods different, and even opposite. Unfortunately, it was impossible to determine the upper limit of numbers in the driest plot, i.e., plot I, because of its location in the habitat moisture gradient outside the habitat optimum boundaries, determined by the actual range of variation of air humidity. From the curves in Figure 4 one might expect that in plot I this limit should be about 45 individuals/dcm², but this would require a very high level of air humidity of the order

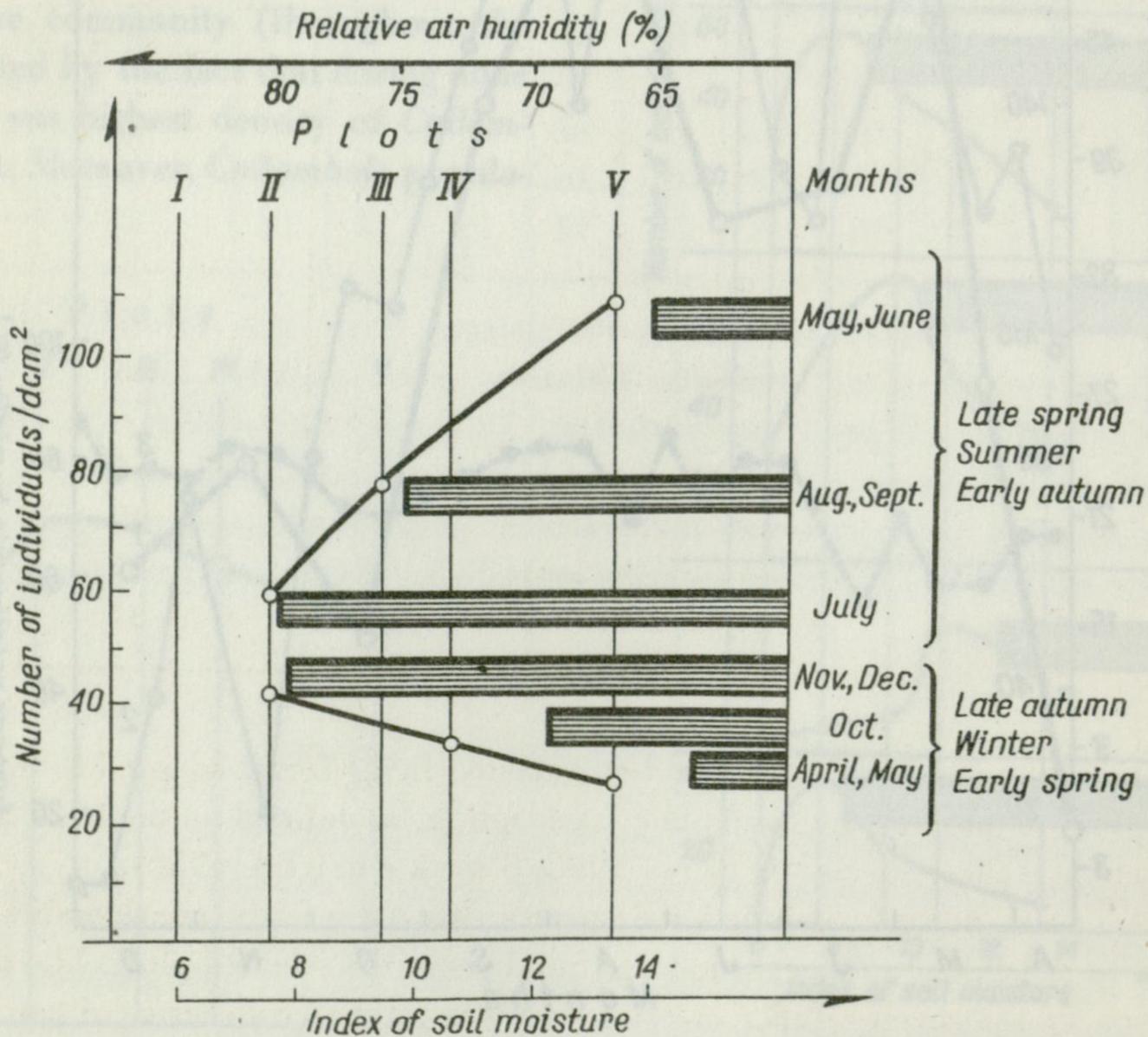


Fig. 4. Variations in the location of maximum density of *Collembola* in different periods (from April to December) against habitat moisture and the average diurnal relative air humidity
Shaded rectangles — average diurnal relative air humidity during the ten-day period preceding the catches

of 85% throughout the 10-days' period, and such a level was never recorded during the study period. However, this would be a very bold supposition in view of the lack of any sufficient ground for such an extrapolation, and it has only been mentioned here in order to additionally visualize the relation between the habitat optimum and population density and its upper range.

5. SPECIES DENSITY

5.1. Habitat preference and degree of species specialization

Like most soil mesofauna aerobionts, the majority of *Collembola* lives in the top 5 cm layer of the forest soil. However, the population density of the different species varies from layer to layer. In the vertical distribution of numbers of the nine dominant *Collembola* species in the forest under research considerable variations of density could be seen: the density of *T. krausbaueri* (a species with strongest tendency to occur in deeper layers) in the litter was almost three times as high as in the mineral soil layer, the population density of *L. lanuginosus* in the litter was about thirty times higher, while *O. bifasciata* showed a hundred-fold prevalence in the litter (Tab. VI).

Tab. VI. Index of species tendency to occur in deeper layers of soil (percentage ratio of density in soil to density in the litter)

Group	Species	Index value
Atmobios	<i>Orchesella bifasciata</i>	<1
	<i>Lepidocyrtus lanuginosus</i>	3
Hemiedaphon	<i>Isotoma notabilis</i>	6
	<i>Anurophorus laricis</i>	7
	<i>Folsomia quadrioculata</i>	15
Euedaphon	<i>Isotomiella minor</i>	12
	<i>Anurida pygmaea</i>	18
	<i>Willemia anophthalma</i>	22
	<i>Tullbergia krausbaueri</i>	37

These findings correspond with the distinguished living-forms adapted to living in the soil at various depths – atmobios, hemiedaphon, euedaphon, as defined on the basis of the morphological characters of these species (Gisin 1943, Bockemühl 1956).

The population density of individual species showed a fairly considerable differentiation, manifested by a tendency to occur in large numbers in the selected plots. The degree of habitat specialization of the species under investigation was estimated in terms of percentage values of the standard deviation, using the formula:

$$S = \frac{100}{\bar{a}} \sqrt{\frac{1}{n} \sum_{i=1}^n (a_i - \bar{a})^2} \quad (3)$$

where: n – number of plots, a_i – population density of species A in the given plot, with $i = 1, 2, 3, \dots, n$, \bar{a} – average population density of species A for the plot.

The value of the specialization coefficient thus calculated increases from zero (equal density of the species in all plots, i.e., a minimum habitat specialization) up to the maximum values, that is, when the population occurs in very large numbers only on one plot (a high habitat specialization). This of course is a relative coefficient, and its numerical values are only comparable within the given range of plots.

On the basis of the calculated values of the coefficient, four species become distinct – *A. laricis*, *A. pygmaea*, *F. quadrioculata*, and *O. bifasciata* – as species of a fairly high habitat specialization, while the following three species – *W. anophthalma*, *I. minor*, *L. lanuginosus* – appeared to be least specialized for the range of habitat conditions of the study. A medium level of specialization could be seen in *I. notabilis* and *T. krausbaueri* (Tab. VII).

Tab. VII. Index of habitat specialization of individual species

Species	Index value
<i>Willemia anophthalma</i>	21
<i>Isotomiella minor</i>	22
<i>Lepidocyrtus lanuginosus</i>	37
<i>Tullbergia krausbaueri</i>	50
<i>Isotoma notabilis</i>	57
<i>Orchesella bifasciata</i>	78
<i>Folsomia quadrioculata</i>	82
<i>Anurida pygmaea</i>	90
<i>Anurophorus laricis</i>	121

The population density curves of individual species show essentially two different types of their course over the soil moisture gradient: with a peak corresponding to one of the plots, or with peaks corresponding to the plots with extremely different conditions (Fig. 5). The first type is represented by the above-named four species with the highest values of the habitat specialization ratio, and by *I. notabilis*. Further in the paper these will be referred to as oligovalent species. The second type is represented by the three species with the lowest habitat specialization, and by *T. krausbaueri*, later on referred to as polyvalent species.

Both among the oligovalent and polyvalent species there are representatives of groups with various predispositions of vertical distribution in the soil.

Noteworthy is the very regular course of population density curves of oligovalent species with a clear symmetry in relation to the density peak, permitting the statement that this peak indicates the position of optimum moisture in the plot gradient.

On this basis it may be assumed that *A. laricis* and *A. pygmaea* show a high preference to drier plots (they will, therefore, be later on referred to as xerophilous), *F. quadrioculata* – a preference to moister plots (a hygrophilous species), whereas *I. notabilis* and *O. bifasciata* – to habitats of intermediate moisture.

The above statement on the extreme requirements of *A. laricis* and *F. quadrioculata*, as regards soil moisture, agrees with the laboratory findings reported by Agrell (1941) concerning the optimum moisture of these species.

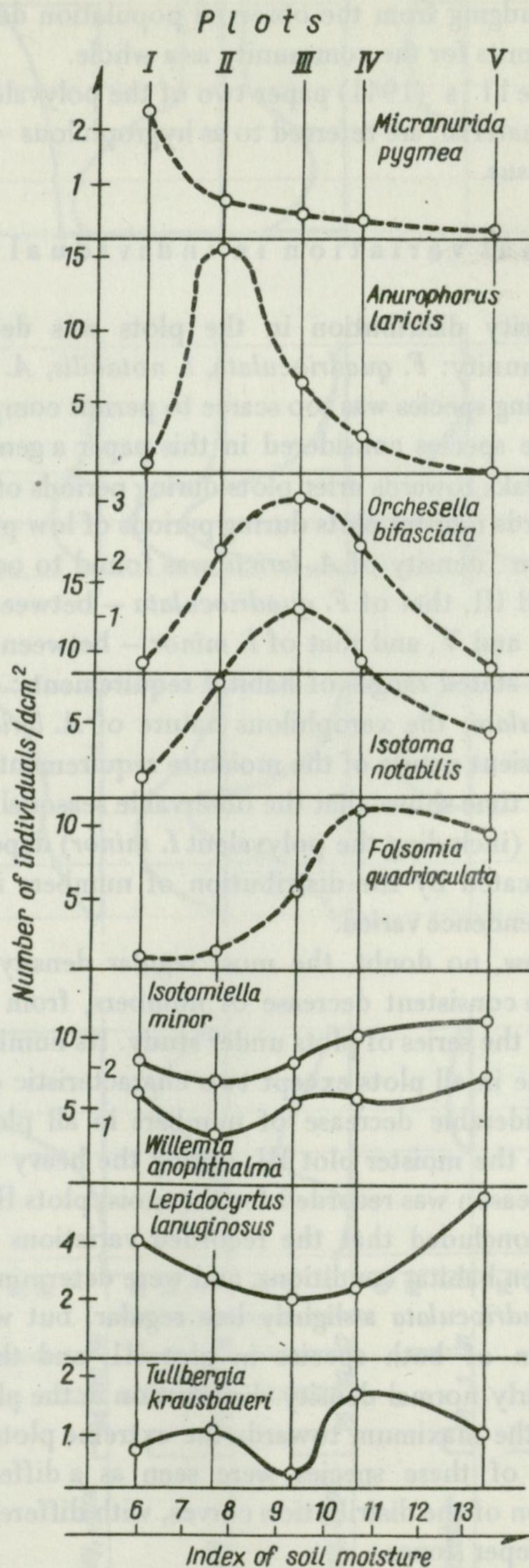


Fig. 5. Average density of *Collembola* species against a gradient of habitat moisture (broken lines — oligo-valent species, continuous lines — polyvalent species)

For the polyvalent species the highest densities were recorded in the two extreme plots of the gradient, outside the optimum moisture of the community (cf. Chapter 4), which indicates their high tolerance in relation to moisture, but does not determine the actual position of the moisture optimum, which – judging from the observed population density distribution – probably is within the optimum limits for the community as a whole.

In the above-quoted Agrell's (1941) paper two of the polyvalent species, which appear to be most numerous in our material, are referred to as hygrophilous – *I. minor*, and a dryness-resistant species – *L. lanuginosus*.

5.2. Seasonal variation in individual plots

Seasonal variation in density distribution in the plots was determined for four most abundant species of the community: *F. quadrioculata*, *I. notabilis*, *A. laricis* and *I. minor* (Fig. 6). The material of the remaining species was too scarce to permit comparisons in time scale.

In the behaviour of all the species considered in this paper a generally consistent shifting could be seen of the density peaks towards drier plots during periods of heavy precipitation and a high air humidity, and towards moister plots during periods of low precipitation and a low air humidity. The peak population density of *A. laricis* was found to oscillate, depending on the moisture, between plots II and III, that of *F. quadrioculata* – between plots III and V, that of *I. notabilis* – between plots II and V, and that of *I. minor* – between plots I and V, which, in general, agrees with the above stated ranges of habitat requirements: confirming the hygrophilous tendency of *F. quadrioculata*, the xerophilous nature of *A. laricis*, the widest tolerance range of *I. minor*, and the transient nature of the moisture requirements of *I. notabilis*.

This regularity at the same time shows that the observable seasonal variations of numbers of each of the species concerned (including the polyvalent *I. minor*) depended on the moisture of the habitat. However, as indicated by the distribution of numbers in the plots in individual periods, the degree of this dependence varied.

A. laricis continued to show, no doubt, the most regular density distribution. During all periods this species showed a consistent decrease of numbers, from the highest-density plot towards both the extremes of the series of plots under study. Its numbers, being highest in plot II, regularly changed with time in all plots except two characteristic cases: during the drought in October there was a considerable decrease of numbers in all plots, the peak population density having been moved to the moister plot III; during the heavy rains in July, the highest reduction in numbers for the season was recorded for the moist plots III and IV.

It should, therefore, be concluded that the recorded variations of numbers of *A. laricis* depended primarily on the given habitat conditions, and were determined by them.

For *I. notabilis* and *F. quadrioculata* a slightly less regular, but with few exceptions (the November density breakdown of both species in plot III, and the August emergence of *F. quadrioculata* in plot I), fairly normal density distribution in the plots was recorded, that is, a steady fall of density from the maximum towards the extreme plots in the gradient. The less regular density distributions of these species were seen as a different, greater than that recorded for *A. laricis*, variation of the distribution curves, with different peaks in the particular periods, and with flatter or steeper slopes.

It may be presumed that the density variations recorded for *F. quadrioculata* and *I. notabilis* to a considerable extent depended on moisture, but the population density in individual plots was much affected also by other environmental factors.

Finally, for the polyvalent species *I. minor* a normal density distribution in the plots was

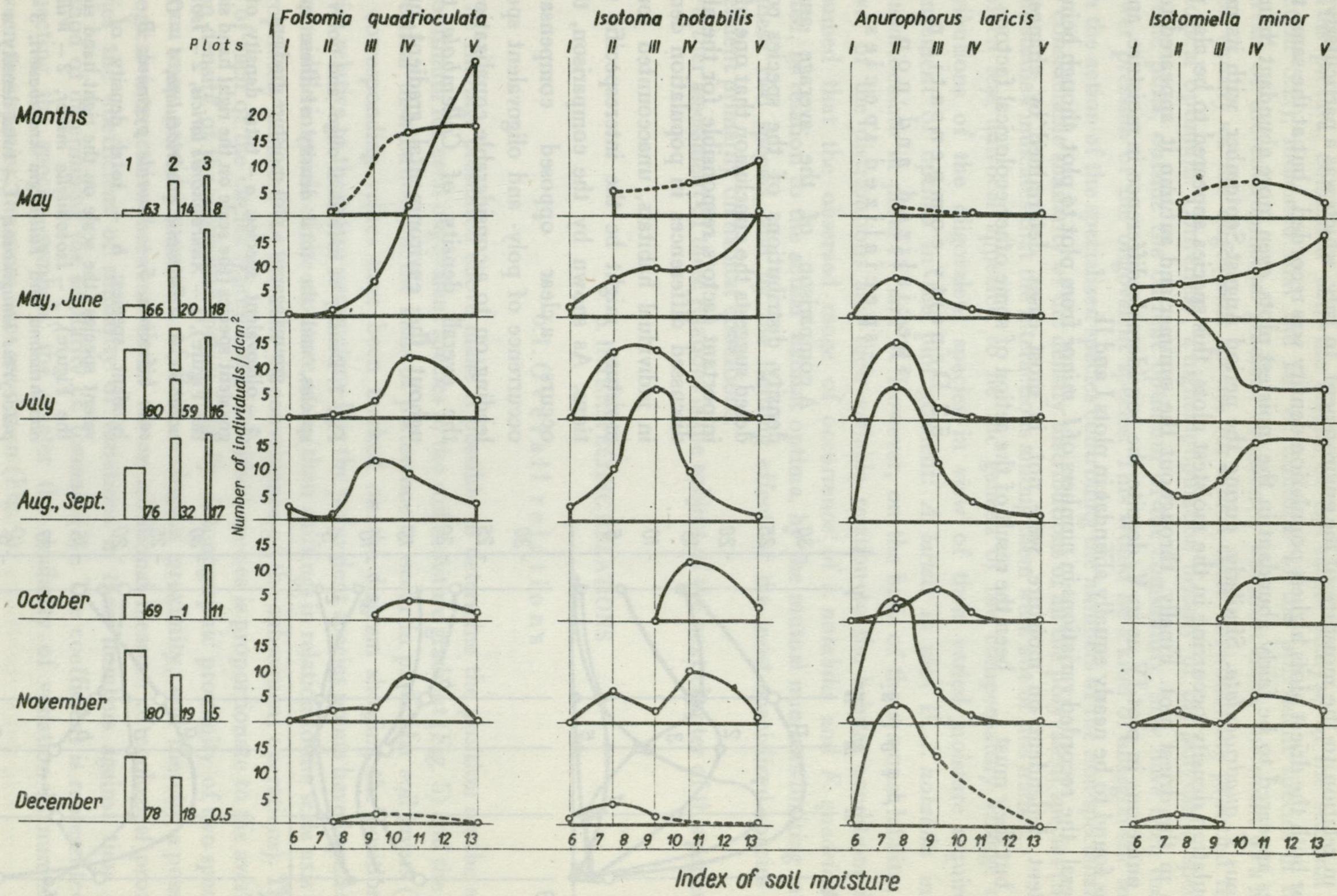
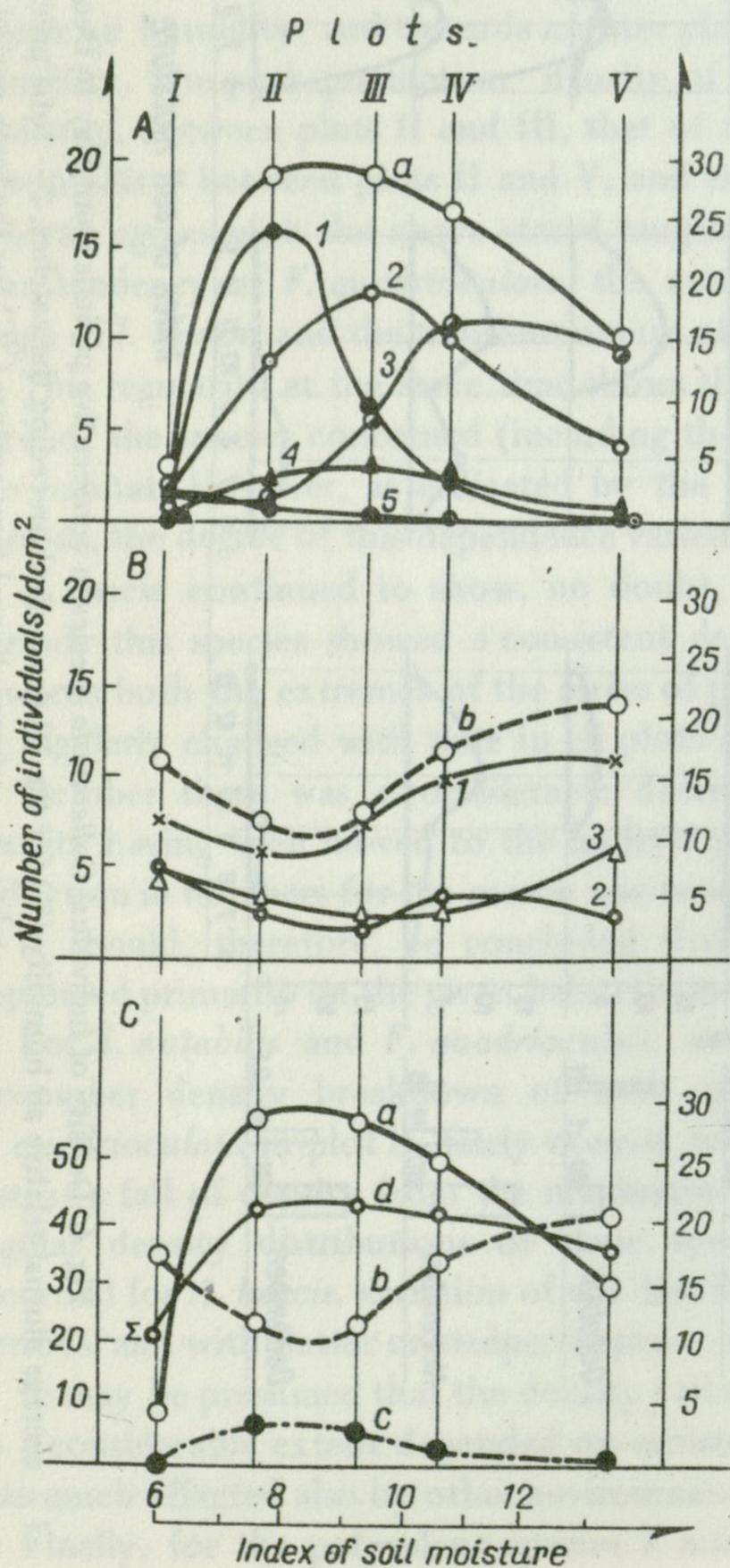


Fig. 6. Density of individual *Collembola* species in consecutive periods from May to December against a plot-moisture gradient
 1 – average diurnal relative air humidity (%) for the 10-day period preceding the catches, 2 – total precipitation (mm) for the 10-day period preceding the catches, 3 – average diurnal temperature (°C) for the same period as above

only recorded in spring (a regular increase of density from plot I to plot V). In other periods — with the general tendency being for the maximum density in dry areas to occur in a wet period, and in the moist areas in a dry period — the population density of individual plots showed little regularity in relation to the moisture of the environment. In July, which was a particularly wet month, for both the driest plots highest population density was recorded, but at the same time the species appeared to be fairly abundant in the moistest plots, even more abundant than the hygrophilous *F. quadrioculata*. Similarly, during the period August-September, with its maximum population density occurring in the moistest plots, this species appeared to be also very numerous in the driest plot. Finally, throughout the summer and autumn it appeared to be almost as numerous in plot IV as in V, despite the considerable difference in moisture, and in July it was found to be nearly equally abundant in plots I and II.

In general, the recorded variations in numbers of *I. minor* from plot to plot, though being to some extent dependent on moisture, were not, in most cases, determined by changes in moisture, but they must have been the result of the action of some other ecological factors.

5.2. Density compensation of specialized and non-specialized species



A comparison of the average annual density distributions of the species considered suggests the conclusion that one of the important factors responsible for the above discussed differences in population density in individual habitats, unaccounted for by moisture, might be the interspecific relations. As shown by the comparison, there occurs a clear opposed compensatory occurrence of poly- and oligovalent species leading on to a considerable equalization of the overall density of *Collembola* throughout the environmental gradient under

Fig. 7. Density of individual oligo- and polyvalent species, and the total density of these species groups against a plot-moisture gradient

A — oligovalent species: a — total density of oligovalent species (the scale on the right hand side of the Figure), 1 — *Anurophorus laricis*, 2 — *Isotoma notabilis*, 3 — *Folsomia quadrioculata*, 4 — *Orchesella bifasciata*, 5 — *Anurida pygmaea*; B — polyvalent species: b — total density of polyvalent species (the scale on the right hand side of the Figure), 1 — *Isotomiella minor*, 2 — *Willemia anophthalma* and *Tullbergia krausbaueri*, 3 — *Lepidocyrtus lanuginosus*; C — total density: a — oligovalent species, b — polyvalent species, c — accessory species (the scale on the right hand side of the Figure), d — total density of all *Collembola* species

study (Fig. 7), as well as a compensatory staggering of the density peaks of individual oligovalent species, due to which their overall density becomes fairly even under the optimum conditions of the habitat gradient (in plots from II to IV) (Fig. 7).

This picture, combined with the results of the earlier analysis of the seasonal variations (Section 5.2.), indicated that the fall of numbers of the polyvalent species in the middle intervals of the environmental gradient considered was most likely the result of a high population density of the oligovalent species for which these environments provided the current ecological optimum. Conversely, a higher population density of the polyvalent species in the extreme plots, outside the current optimum of the community, may have been the result of a lower pressure of the oligovalent species. This would be a kind of antagonistic interaction, with the action of the specialized species controlling the numbers of the non-specialized species. The considerable similarity of the density distributions of all the polyvalent species (non-specialized) studied indicates that the interactions among them were not of this nature.

Much less univocal appeared to be the genesis of the compensatory change of density distributions of the oligovalent species in view of their varied moisture requirements — arrangement of optima in the plot gradient: *A. laricis* in plot II, *I. notabilis* in plot III, *F. quadrioculata* in plots IV and V. However, on the basis of the seasonal lability, discussed above, of the distributions and their variable relation to the habitat conditions it may be presumed that the observed range of occurrence of *I. notabilis* and *F. quadrioculata* was limited, in relation to the actual habitat optima, by the mutual numbers-limiting interactions of these two species, and by the limiting effect of the most specialized species *A. laricis*, dependent primarily on habitat conditions.

Further assessment of these relations is the subject of the next chapter of this paper.

6. INTERSPECIFIC RELATIONS

6.1. Overall relations

The findings presented above make it possible to determine the position on the schema of the optimum for each oligovalent species in the soil moisture gradient (Fig. 5) and the optimum of vertical distribution on the basis of preference to occur in particular soil layers (Tab. VI). The corresponding values have been marked on the diagram showing the position of each species relative to these two parameters. For the polyvalent species points have been established in the middle intervals of the moisture scale (their shiftings in relation to the scale axis have been appropriately adjusted for the sake of convenience of the subsequent operations). The surface area of each of the circles representing individual species is proportionate to the average population density of the particular species (Fig. 8). A topographic proximity of two species in the diagram may provide a measure of their ecological proximity, and thereby a possibility of ecological interactions between them. As an additional measure of ecological proximity of species the coefficient of similarity of variations in their numbers against time was used [method of determining the similarity cf. formula (2)]. The coefficient is represented by lines connecting the species symbols; the greater the similarity of variation in numbers found between two species, the more lines are drawn (Fig. 9).

The comparison of the coefficient of similarity in the variation of numbers of each pair of species in time gives a fairly clear picture (Fig. 9). A high similarity can be seen between the more xerophilous oligovalent — *A. laricis*, *O. bifasciata*, and the polyvalent species *L. lanuginosus*

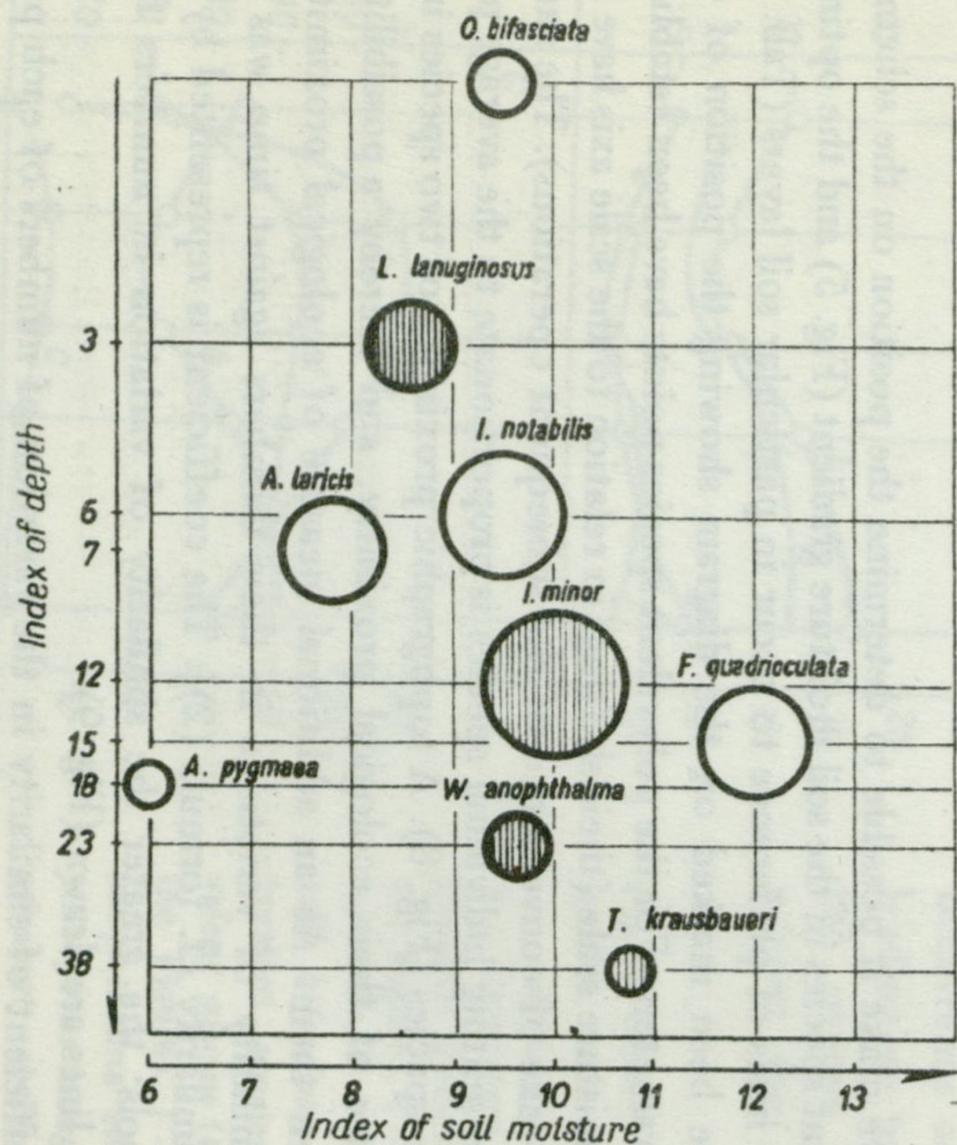


Fig. 8. A diagram of the distribution of the *Collembola* species under study

Shaded circles – polyvalent species, circles – oligovalent species; the surface area of all circles is directly proportionate to the density of the species

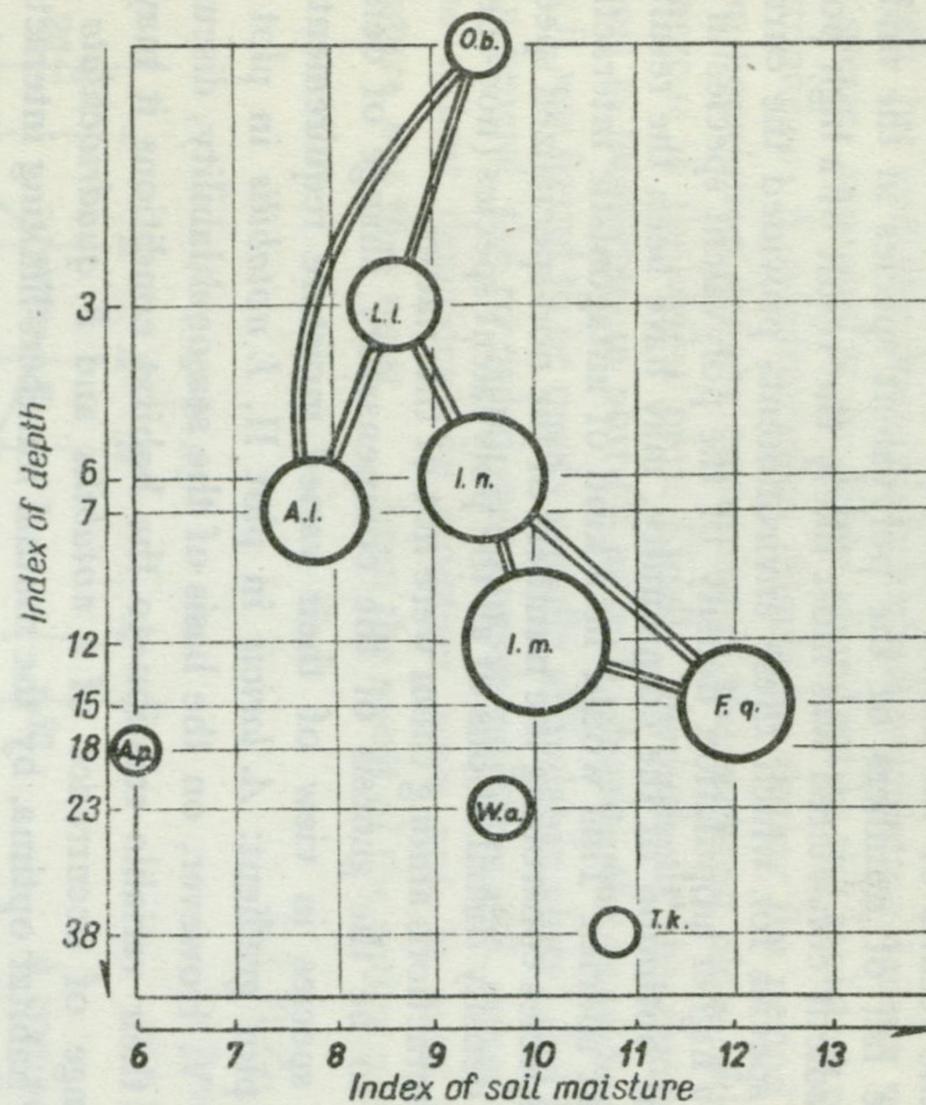


Fig. 9. Similarity in density variations of the *Collembola* species throughout the study period [determined according to formula (2)] against their distribution

One line connecting the species – similarity coefficient value 0.15–0.24, two lines connecting the species – similarity coefficient value 0.25–0.39, three lines connecting the species – similarity coefficient value 0.40–1.0 (used in explanations to further Figures). *O.b.* – *O. bifasciata*, *L.l.* – *L. lanuginosus*, *A.l.* – *A. laricis*, *I.n.* – *I. notabilis*, *I.m.* – *I. minor*, *F.q.* – *F. quadrioculata*, *A.p.* – *A. pygmaea*, *W.a.* – *W. anophthalma*, *T.k.* – *T. krausbaueri*

[as indicated by its autecological data, this is a drought resistant species – Agrell (1941)]. Another group of similar variations in numbers against time is made up of the rather hygrophilous species – the oligovalent species *F. quadrioculata*, *I. notabilis*, and the polyvalent species *I. minor* [as indicated by autecological data, this too is a hygrophilous species – Agrell (1941)]. These two groups are connected by a certain degree of similarity in the variation of density against time of the species: *I. notabilis* and *L. lanuginosus*. The remainder of the species show little similarity in density variations against time.

The fact that among species that have similar moisture requirements there also exist similar reactions in variation of numbers, additionally indicates their particularly close ecological relationship, and thereby the possibility of competitive relations occurring among them.

6.2. Relations within individual plots

When analysing the interspecific relations in individual plots we assume that if species of very similar environmental requirements (e.g., hygrophilous, of very similar density responses to phenological changes) avoid one another in the samples, this indicates that there exist antagonistic relations among them.

A trial was made to find whether such relations really existed. For this purpose an analysis of the coincidence of species in samples using the “each with each” combination was carried out. The material was analysed by means of Forbes (1907) coincidence coefficient

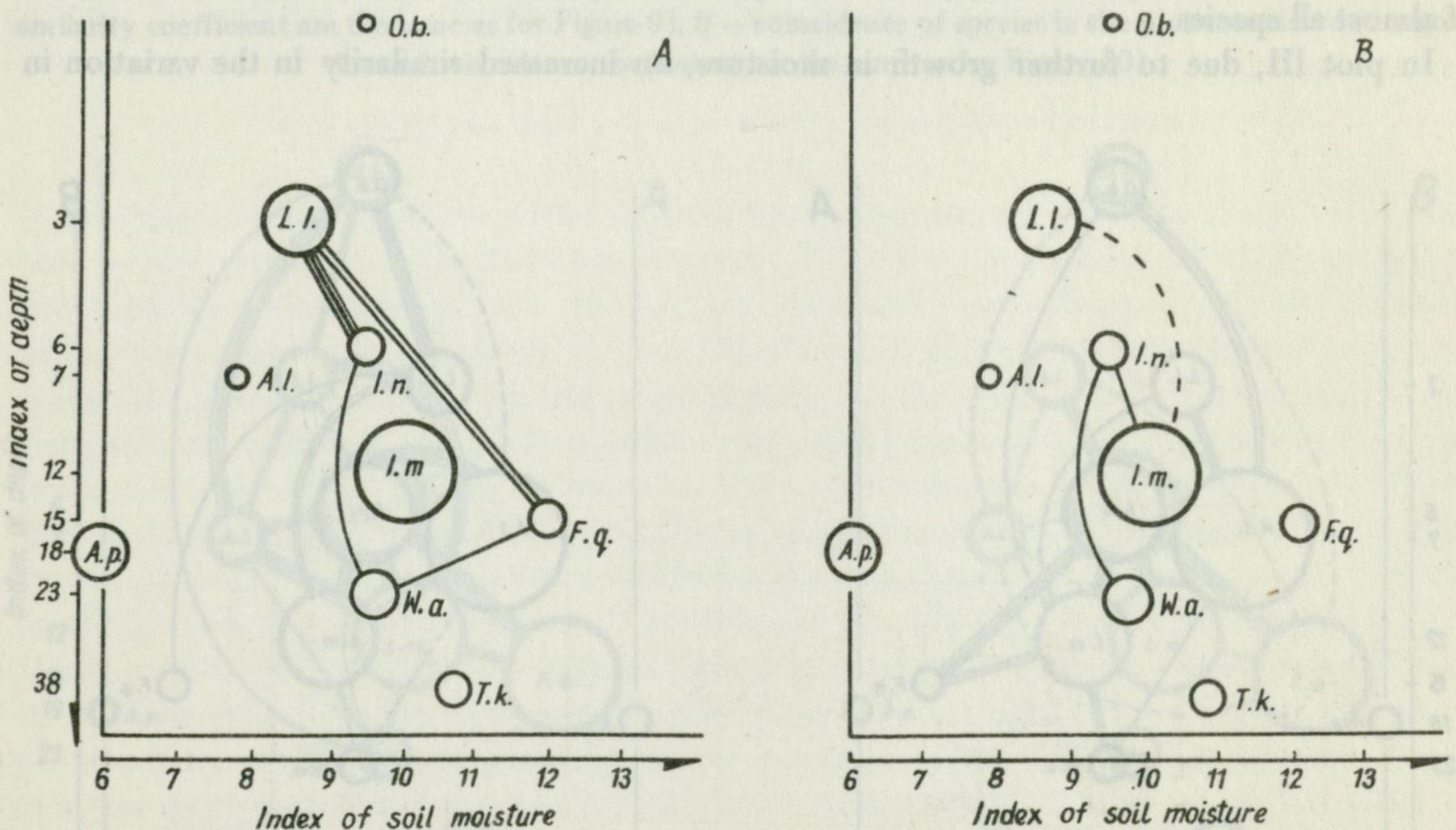


Fig. 10. Interspecific relations in plot I against species distribution

A – similarities in density variation of the species throughout the study period (species designation and the similarity coefficient values are the same as for Figure 9), B – species coincidence in the plot considered (continuous lines – territorial convergence: one line connecting the species – convergence coefficient value 2–3, two lines – coefficient value 4, three lines – coefficient value 5–7 (two-three lines used in the explanations to further Figures); broken lines – territorial divergence: one line connecting the species – coefficient value 0.3–0.5, two lines – coefficient value – 0.2, three lines – coefficient value 0.1 (two-three lines used in the explanations to further Figures); absence of connections – independent occurrence of species

[formula (1)] in the following order: (1) for each pair of species the coefficient value was calculated for every point of time in every plot, (2) the numerical data obtained for each species pair were represented as the number of territorially convergent and the number of territorially divergent occurrences in individual plots throughout the given period of time, (3) by dividing the number of territorially convergent occurrences by the number of territorially divergent occurrences in the samples the final result was obtained indicating the predominating tendency in a given pair of species. Only those results were taken into account in which the predominance of a particular tendency was very clear (the value of the ratio being greater than 2, or less than 0.5). All other cases were considered to be independent occurrences of species.

The driest plot, plot I, where a very low population density was seen throughout the study period, did not supply any data which would make it possible to draw conclusions concerning the behaviour of even the most abundant species (Fig. 10). It may only be stated that there was a certain degree of similarity in the variation of numbers with time between *L. lanuginosus* and *I. notabilis*, and between *L. lanuginosus* and *F. quadrioculata*. These species do not show any tendency towards territorial convergence, and more often than not their coincidence is only accidental. A tendency toward territorial divergence can be seen between *L. lanuginosus* and *I. minor*, which may result from their environmental requirements being different.

In the next plot, plot II, being slightly more moist, more marked similarities in density variations in time can be seen (Fig. 11) among both the xerophilous and hygrophilous species. Territorially, the species of both these groups tend to avoid *A. laricis* which dominates there numerically. The most hygrophilous species — *F. quadrioculata* — occurs there independently of almost all species.

In plot III, due to further growth in moisture, an increased similarity in the variation in

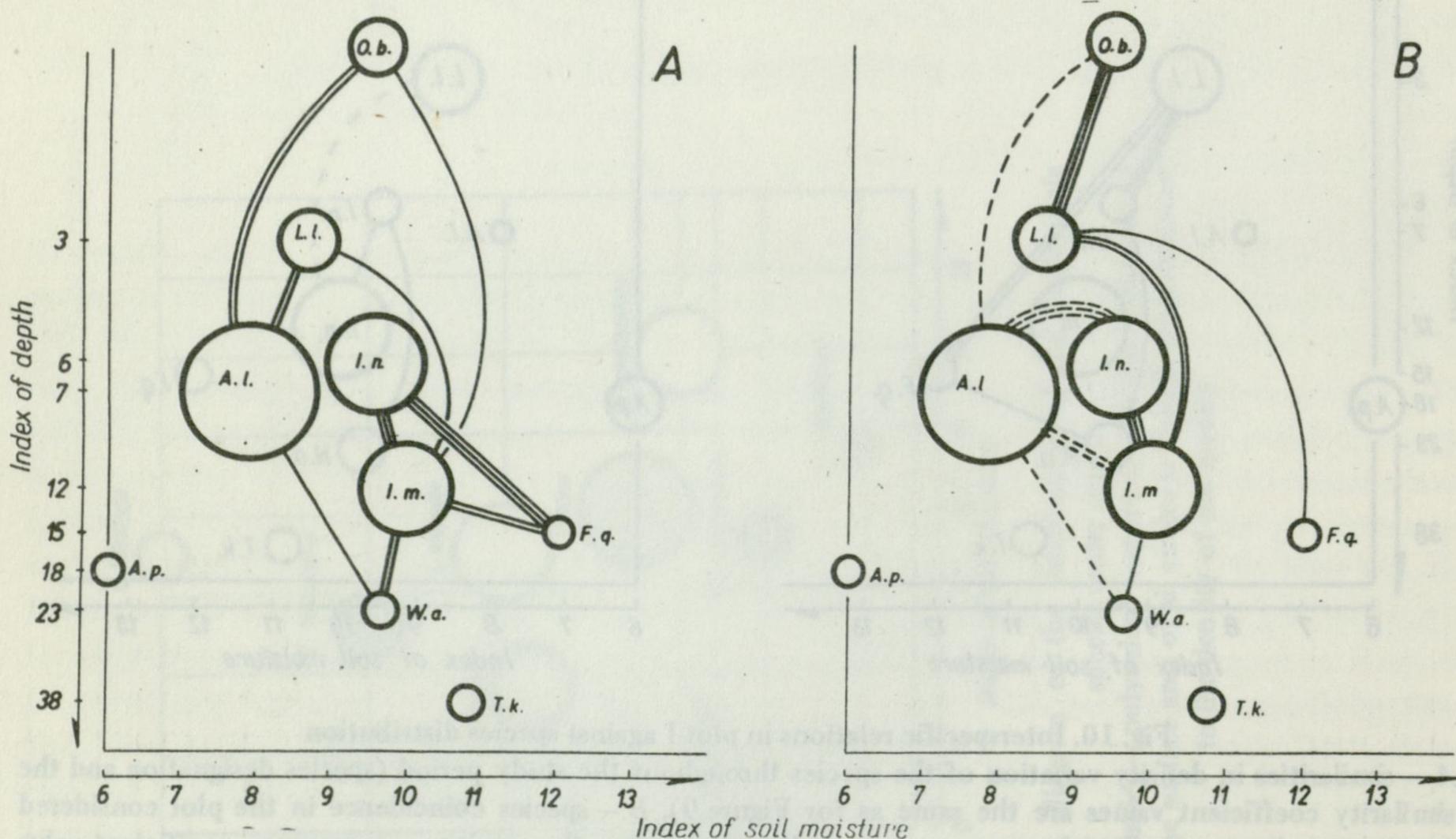


Fig. 11. Interspecific relations in plot II against species distribution

A — similarities in density variation of the species throughout the study period (designation of species and similarity coefficient values are the same as for Figure 9), B — coincidence of species in the plot considered (designations of coincidence coefficient are the same as for Figure 10)

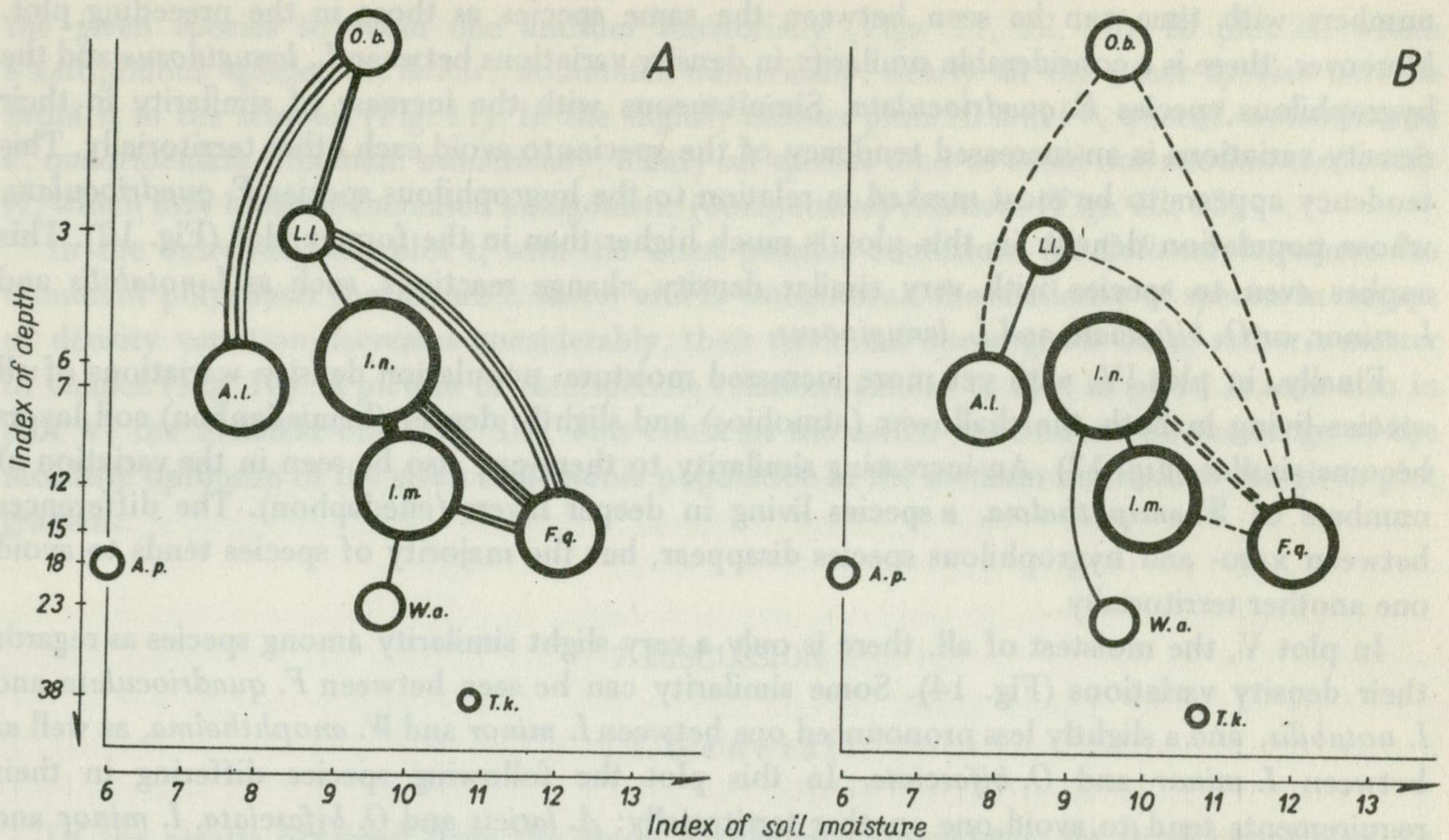


Fig. 12. Interspecific relations in plot III against species distribution

A – similarities in density variation of the species throughout the study period (designations of species and of similarity coefficient are the same as for Figure 9), B – coincidence of species in the plot considered (designations of coincidence coefficient are the same as for Figure 10)

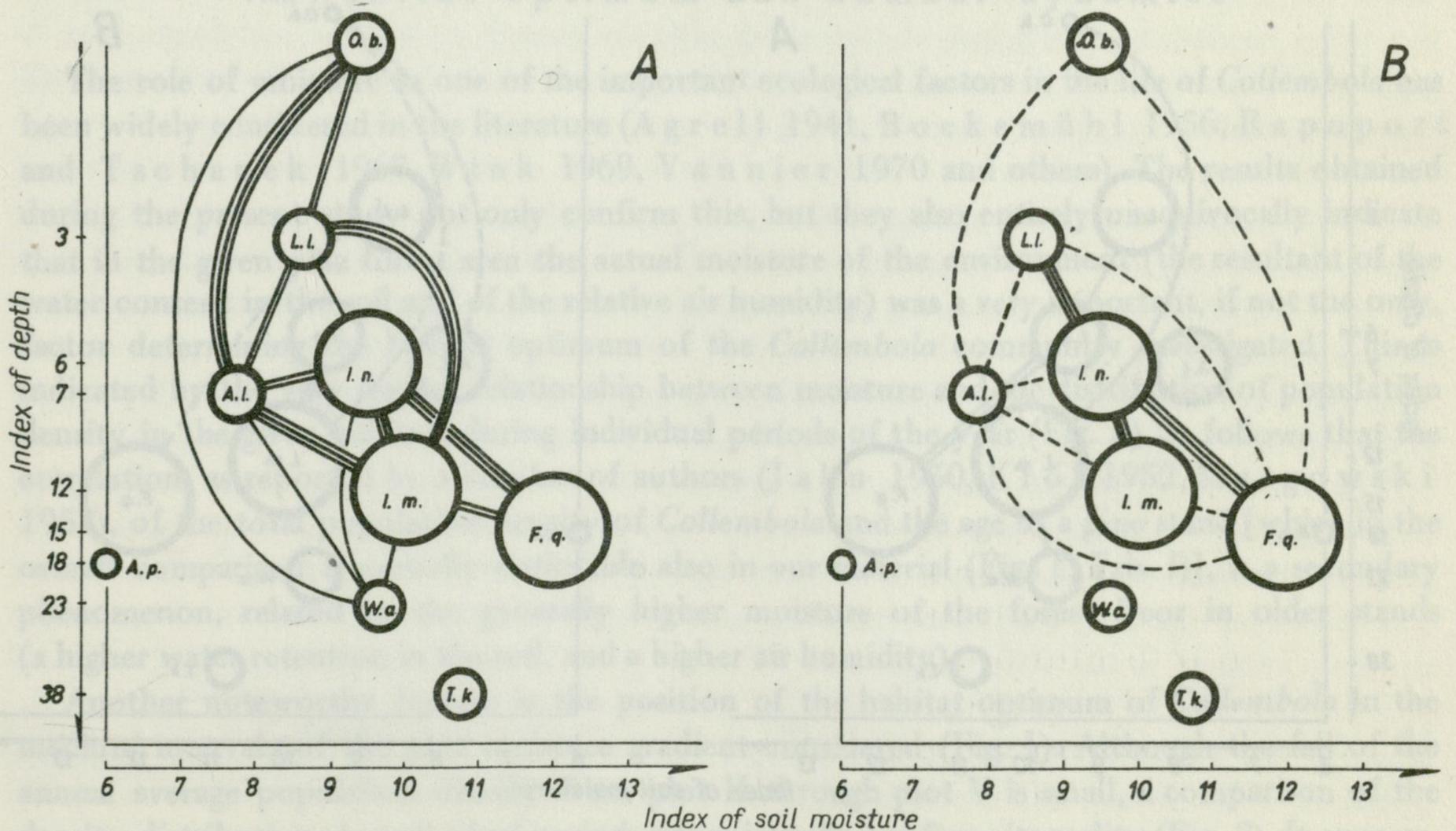


Fig. 13. Interspecific relations in plot IV against species distribution

A – similarities in variation of species density throughout the study period (designations of species and similarity coefficient are the same as for Figure 9), B – coincidence of species in the plot considered (designations of coincidence coefficient are the same as for Figure 10)

numbers with time can be seen between the same species as those in the preceding plot. Moreover, there is a considerable similarity in density variations between *L. lanuginosus* and the hygrophilous species *F. quadrioculata*. Simultaneous with the increase of similarity in their density variations is an increased tendency of the species to avoid each other territorially. This tendency appears to be most marked in relation to the hygrophilous species *F. quadrioculata*, whose population density in this plot is much higher than in the former plot (Fig. 12). This applies even to species with very similar density change reactions, such as *I. notabilis* and *I. minor*, or *O. bifasciata* and *L. lanuginosus*.

Finally, in plot IV, with yet more increased moisture, population density variations of all species living in both the shallower (atmobios) and slightly deeper (hemiedaphon) soil layers become similar (Fig. 13). An increasing similarity to them can also be seen in the variation of numbers of *W. anophthalma*, a species living in deeper layers (euedaphon). The differences between xero- and hygrophilous species disappear, but the majority of species tends to avoid one another territorially.

In plot V, the moistest of all, there is only a very slight similarity among species as regards their density variations (Fig. 14). Some similarity can be seen between *F. quadrioculata* and *I. notabilis*, and a slightly less pronounced one between *I. minor* and *W. anophthalma*, as well as between *I. minor* and *O. bifasciata*. In this plot the following species differing in their requirements tend to avoid one another territorially: *A. laricis* and *O. bifasciata*, *I. minor* and *O. bifasciata*, and *L. lanuginosus* and *F. quadrioculata*.

To sum up, in plots II, III, IV, where there were, as assessed by an earlier analysis, optimum conditions for *Collembola*, there was a considerable similarity in their variation of numbers with phenological changes, and the greater the similarity, the more marked is the tendency of

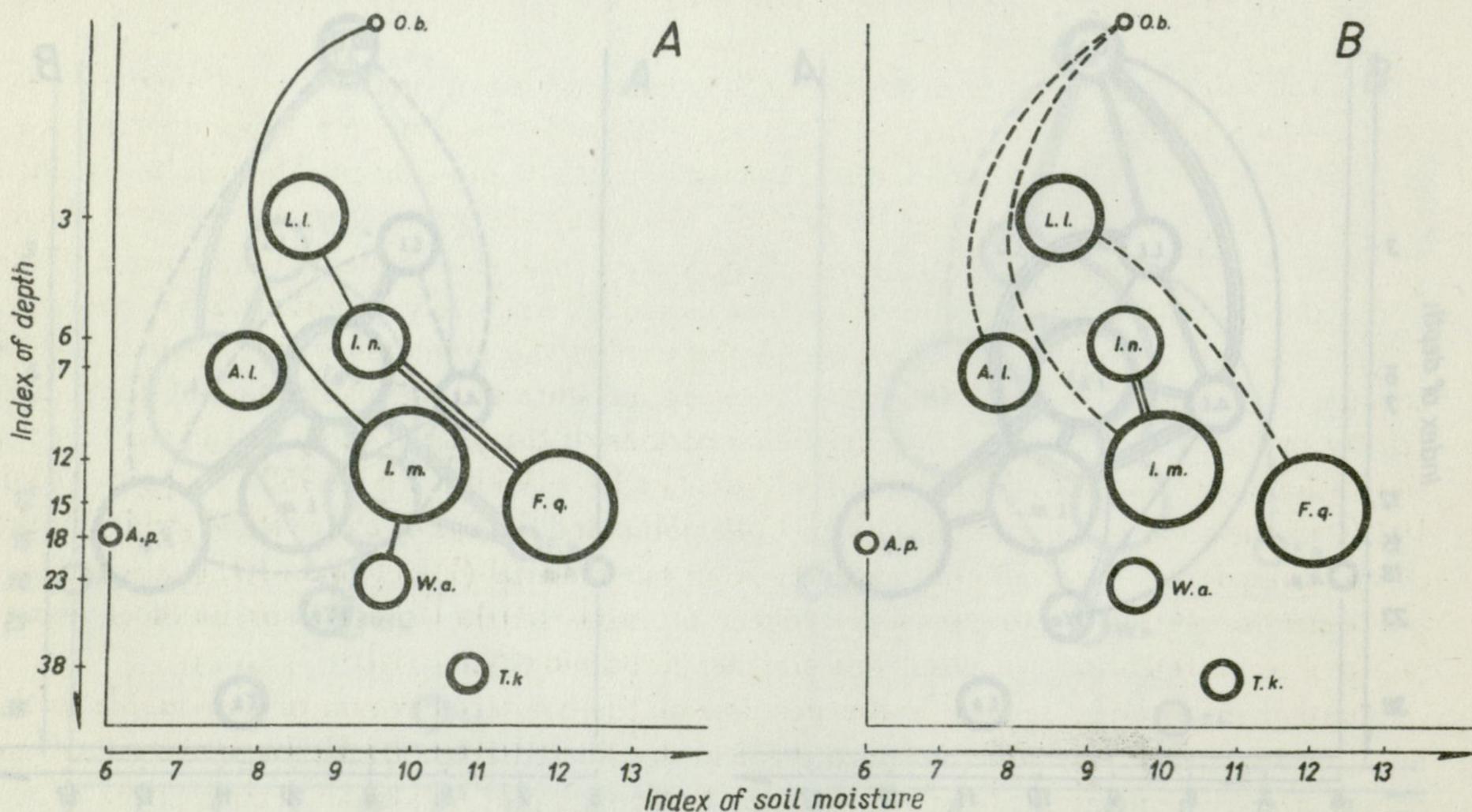


Fig. 14. Interspecific relations in plot V against species distribution

A — similarities in the variation of species density throughout the study period (designations of species and similarity coefficient are the same as for Figure 9), B — coincidence of species in the plot considered (designations of coincidence coefficient are the same as for Figure 10)

the given species to avoid one another territorially (Figs. 11, 12, 13). In plot II, where a xerophilous species, *A. laricis*, dominates numerically, nearly all the other species tend to avoid it in the samples (Fig. 11). In the slightly moister plots III and IV, where *I. notabilis* and *F. quadrioculata* dominate numerically, nearly all species tend to avoid one another territorially, which may indicate increased antagonistic (competitive) relations (Figs. 12, 13).

In the extremely dry plot I, with the worst possible conditions for *Collembola*, where the dominant polyvalent species are *I. minor* and *L. lanuginosus*, the similarity of species in respect of density variation decreases considerably, their territorial convergence being rather a matter of chance (Fig. 10). A picture of interspecific relations similar to that in plot I is seen also in plot V, the moistest one (Fig. 14). This confirms the earlier conclusions on the range of the moisture optimum of the given *Collembola* population in the medium intervals of the given plot gradient.

7. DISCUSSION

7.1. General

Of the results obtained from the study particularly noteworthy are those concerning the following: (1) moisture and temperature as environmental factors determining the habitat optimum and affecting the variation of numbers of *Collembola* over the yearly cycle, and (2) interspecific relations as a density-control factor of the community.

7.2. Habitat optimum and number dynamics

The role of moisture as one of the important ecological factors in the life of *Collembola* has been widely considered in the literature (Agrell 1941, Bockemühl 1956, Rapoport and Tschapek 1967, Wink 1969, Vannier 1970 and others). The results obtained during the present study not only confirm this, but they also entirely unequivocally indicate that in the given pine forest area the actual moisture of the environment (the resultant of the water content in the soil and of the relative air humidity) was a very important, if not the only, factor determining the habitat optimum of the *Collembola* community investigated. This is indicated by the very regular relationship between moisture and the distribution of population density in the given habitats during individual periods of the year (Fig. 2). It follows that the correlation, as reported by a number of authors (Jahn 1950, Król 1952, Margowski 1952), of the total population density of *Collembola* and the age of a pine stand [which in the overall comparison is partially noticeable also in our material (Fig. 1, Tab. I)], is a secondary phenomenon, related to the generally higher moisture of the forest floor in older stands (a higher water retention in the soil, and a higher air humidity).

Another noteworthy feature is the position of the habitat optimum of *Collembola* in the medium intervals of the plot moisture gradient considered (Fig. 1). Although the fall of the annual average population density from plot II through plot V is small, a comparison of the density distributions in individual periods unequivocally confirms its reality (Fig. 2). It appears, therefore, that plot III already was at times too moist for *Collembola*, which finding seems to be quite surprising. Although some experimental studies (Agrell 1941, Vannier 1970), as well as some field investigations (Agrell 1941, Hammer 1944, M. Kaczmarek 1973) in fact indicate that there exists an upper limit in the soil-moisture tolerance of

Collembola, this limit is within the range of 40–80% water content in the soil, or is connected with a seasonal flooding of the given area by excess precipitation waters. The range of soil moisture, characteristic of a fresh pine forest, and especially with the deep ground-water horizon of the study area, is much below the values quoted, hence one should always expect highest densities of *Collembola* to occur in the moistest plot V. Possibly, there may be some local differences in the ecological requirements of the same *Collembola* species in dry and moist areas, which would require a separate analysis. The possibility of such an interpretation is indicated by Agrell's (1941) experiments which showed a slightly lower tolerance to excess soil moisture in individuals derived from drier areas.

Against the above-discussed relationship between the habitat optimum and the moisture of the environment characteristic variations of numbers of the *Collembola* species studied could be seen over the yearly cycle. They appeared to depend fairly clearly on temperature, as indicated by the summer density peaks (Fig. 3).

According to the literature, peak population densities of *Collembola* are recorded for the autumn-winter period, or for the summer. This discrepancy of data was the cause of many speculations. In an earlier paper concerning a mixed forest (M. K a c z m a r e k 1963) a suggestion was put forward as regards the relationship between the autumn peak numbers of *Collembola*, observed there, and the litter recovery cycle. The difference in litter recovery cycle between a coniferous forest and a deciduous and mixed forests lies in the fact that the fall of coniferous needles is a protracted process, and so is their decomposition, with a simultaneous high retention, as opposed to the fall of broad-leaves which concentrates in autumn, their rather fast decomposition and a lower retention of the broad-leaved litter. For this reason autumn is not connected with any significant changes in the litter formation cycle in a coniferous forest, where the litter is not subject to any greater fluctuations. The availability of food derived from the fallen needles, to a large extent connected with the growth of bacteria and fungi, is at its highest in summer when the temperature and precipitation are rather high. Under these conditions temperature may play a decisive role for the growth of *Collembola* population, whereas in the deciduous and mixed forests the effect of the leaf-fall cycle may dominate over the effect of temperature on the yearly cycle of *Collembola* population density, hence the autumn-winter population density peaks. This conclusion is confirmed by data from the literature. In fact, in the above quoted studies, as in the present study, the summer density peaks concerned coniferous forests (A g r e l l 1941, P o o l e 1961, J o o s s e 1969), and the autumn-winter peaks were related to deciduous and mixed forests (S c h a l l e r 1949, V o l z 1954), and meadows and pastures (W e i s — F o g h 1948, S h e a l s 1957).

The method of analysis, used in the present study, based on the comparison of the variations in *Collembola* population density occurring over the moisture gradient of the study plots, and the changes of density recorded against the seasonally changing environmental conditions (cf. Section 4.2.) made possible a closer analysis of the distribution of maximum densities attained in the different plots in different periods under the optimum joint action of soil moisture and air humidity on *Collembola*. The comparison has shown (Fig. 4) that with the growing soil moisture in the given plot gradient the maximum possible (attainable with optimum soil-moisture and air-humidity) top level of *Collembola* density increases rapidly during the periods of higher temperature of the full growing season, but drops slightly during the cold seasons.

7.3. Interspecific relations

Collembola are found to rapidly react to a mosaic (patchy) nature of the habitat, and they form distinct concentrations (Glasgow 1939, Macfadyen 1952, Poole 1961, Hughes 1962, Hale 1966, Černova and Čugunova 1967, Usher 1969, Joosse 1970). This is no doubt connected with the known sensitivity of *Collembola* to even small deviations from the optimum conditions of a microhabitat (Gisin 1952, Poole 1964, Černova 1970, Ananeva 1971). The concentration of *Collembola* appears to be correlated with their population density – being highest at minimum density and tending to become uniform at high density [W. Kaczmarek (1960); material from a pine forest, collected from May to December]. The growing tendency toward a uniform occurrence with a growing population density has also been pointed out by Hairston (1959). This process may indicate a direct coincidence of the concentration of individuals and an abundance of microhabitats favourable to the given species, or the existence of some interactions within the population.

Previous studies in this field have also failed to find unequivocally whether competitive relations have any effect on the population density in *Collembola* in the sense of mutual limitation of numbers, or of the space occupied (Christiansen 1967). A fairly clear divergence of territorial occurrence, maybe due to a mutual displacement of species, has so far been recorded only for mobile epigeic forms. The investigations concerned, carried out using traps, have shown a territorial isolation of individual concentrations of the species caught (M. Kaczmarek 1960). Some evidence concerning the existence of this kind of phenomena has been recorded also by Poole (1961), where *I. notabilis* replaced other species.

Much more data has been gathered on the high ecological affinity among different species, as determined by Kulczyński's method (Agrell 1963), by density correlation (Poole 1961), and by the assessment of associations by means of Pearson's formula (Davis 1963, Debauche 1969, McMillan 1969, Usher 1969).

The difficulty in deciding whether there is an active current competition under the conditions of comparative field studies lies primarily in the dilemma of whether it is indicated by the tendency of species to coincide, or possibly by their tendency to avoid one another.

The results of the present study seem to provide some evidence concerning the problem of competition in the given *Collembola* community. They have shown that there are: (1) a compensatory growth of numbers of the polyvalent species at either end of the environmental optimum of this community (Fig. 7), (2) a tendency among a number of species to avoid one another territorially, the latter being true of species with a high, empirically proved for the study area, ecological affinity, and very similar reactions manifested by a similarity of density variations with seasonal changes of the environmental conditions (Figs. 10–14).

I wish to express my sincere thanks to Dr. W. Kaczmarek for his guidance and helpful criticism during the course of this work. My thanks are also due to Dr. T. Wierzbowska for her cooperation in the statistical interpreting the coincidence coefficient.

8. SUMMARY

The present study has been carried out on *Collembola* material derived from a lowland, fresh pine forest of the Lemańsk forest district (Łobodno forest inspectorate). In the study area 5 plots were delimited and arranged into a gradient according to growing soil moisture. From each plot 50 randomly distributed soil

samples, each 10 cm² in surface area, were collected at 2-weeks', or monthly intervals from May to December (Tab. II).

Optimum conditions for the occurrence of *Collembola* were found to exist in the middle interval of the given plot gradient.

The highest population density of *Collembola* in individual periods was found in plots with currently most favourable moisture conditions: in periods of higher precipitation and a higher average air humidity – in plots of lower soil moisture, and during periods of lower precipitation and an accordingly lower average air humidity – in plots with a higher soil moisture (Fig. 2).

Further analysis of the material suggests that the level of numbers of the *Collembola* community depended on the degree of the soil moisture of the plots in the way that during the warm season the maximum population density grew with the increasing soil moisture, while in the cold season it decreased (Fig. 4).

The most numerous species of the community appeared to differ in respect of their habitat specialization (Tab. VII). One of the groups included oligovalent species, abundant only under specific environmental conditions; another group included polyvalent species occurring in equally large numbers under extremely different environmental conditions of the given forest area (Fig. 5). Variations of the average population density of the species groups of these two types in the series of study plots, and in individual periods appeared to be of compensatory nature (Fig. 7). The reproducibility of this process permits the presumption that the population size of oligovalent species depends (proportionately to the degree of their specialization) directly on the habitat conditions. At the same time the population density of the polyvalent species is affected by the density of oligovalent species in the sense that the overall density of the community becomes equalized to a relatively stable level.

From the above the suggestion follows that in the given *Collembola* community there exist interspecific limitations of competitive nature.

The habitat optima of the species under study indicate that the oligovalent group includes hygro- and xerophilous species, and that the species concerned differ in their preference to occur at various depths (Tab. VI, Fig. 8).

Under the optimum conditions of the occurrence of *Collembola* (in plots with non-extremal values of soil moisture for the area) most of the species tended to avoid [formula (1)] the numerically dominant species (Figs. 11–13).

In the given series of study plots (except the extremely moist plot V) the similarity in density variations of the given species [formula (2)] increased with the growth of soil moisture (Figs. 10–13). In the same series of plots also a growing tendency could be observed among the species to avoid one another territorially [formula (1)], which confirms the supposition that among the species studied competitive relations occurred (Figs. 10–13).

9. POLISH SUMMARY (STRESZCZENIE)

Praca została wykonana na materiale *Collembola*, zebrany w nizinym świeżym borze sosnowym w leśnictwie Lemańsk (nadleśnictwo Łobodno). W terenie wyznaczono pięć stanowisk, uszeregowanych w gradiencie wzrastającej wilgotności gleby. Z każdego stanowiska pobierano losowo po 50 prób gleby o powierzchni 10 cm² każda, od maja do grudnia, w odstępach dwutygodniowych lub miesięcznych (tab. II).

Stwierdzono, że optymalne warunki występowania *Collembola* znajdowały się w środkowym przedziale gradientu badanych stanowisk.

W poszczególnych okresach najwyższa liczebność *Collembola* występowała na tych stanowiskach, na których aktualnie ustalały się najbardziej sprzyjające warunki wilgotnościowe: przy większych opadach i wyższej średniej wilgotności powietrza – na stanowiskach o mniejszej wilgotności gleby, przy mniejszych opadach i odpowiednio niższej średniej wilgotności powietrza – na stanowiskach o większej wilgotności gleby (fig. 2).

Dalsza analiza materiału sugeruje, że poziom liczebności zgrupowania *Collembola* był warunkowany stopniem wilgotności gleby na stanowisku w ten sposób, iż w cieplej porze roku maksymalna liczebność rosła wraz ze wzrostem wilgotności gleby, a w porze chłodnej ulegała zmniejszeniu (fig. 4).

Najliczebniejsze gatunki zgrupowania *Collembola* wykazują zróżnicowanie pod względem specjalizacji siedliskowej (tab. VII). Jedną grupę stanowią gatunki oligowalenne, występujące licznie tylko w określonych warunkach środowiskowych, drugą – gatunki poliwalenne, występujące podobnie licznie w skrajnie różnych

warunkach środowiskowych badanego lasu (fig. 5). Wahania średniej liczebności u grup gatunków tych dwu typów w badanym szeregu stanowisk i w poszczególnych okresach mają charakter kompensacyjny (fig. 7). Powtarzalność tego zjawiska pozwala przypuszczać, że liczebność gatunków oligowalentnych jest (proporcjonalnie do stopnia ich specjalizacji) bezpośrednio zależna od badanych warunków siedliskowych. Natomiast liczebność gatunków poliwalentnych kształtuje się w tym czasie zależnie od liczebności gatunków oligowalentnych w ten sposób, że liczebność całego zgrupowania jest wyrównywana do względnie stałego poziomu.

Wynika stąd sugestia, że w badanym zgrupowaniu *Collembola* występują ograniczenia międzygatunkowe typu konkurencji.

Optima siedliskowe badanych gatunków wskazują na istnienie, wśród gatunków oligowalentnych, gatunków wilgocio- i sucholubnych oraz na zróżnicowanie badanych gatunków pod względem preferencji występowania na różnej głębokości (tab. VI, fig. 8).

W optymalnych warunkach do występowania *Collembola* (na stanowiskach o średniej dla badanego terenu wilgotności gleby) u większości gatunków przejawia się tendencja do unikania [wzór (1)] gatunku dominującego liczebnie (fig. 11–13).

W badanym szeregu stanowisk (wyłączywszy skrajnie wilgotne stanowisko V) podobieństwo w zmianach liczebności badanych gatunków [wzór (2)] wzrastało wraz ze wzrostem wilgotności gleby (fig. 10–13). W tym samym szeregu stanowisk wzrastała również tendencja do przestrzennego unikania się gatunków [wzór (1)], co potwierdza przypuszczenie, że między badanymi gatunkami wykształcają się stosunki konkurencyjne (fig. 10–13).

10. REFERENCES

1. Agrell I. 1941 – Zur Ökologie der Collembolen. Untersuchungen in schwedischen Lapland – Opusc. ent. Suppl. III, 132 pp.
2. Agrell I. 1963 – A sociological analysis of soil *Collembola* – *Oikos*, 14: 237–247.
3. Ananova S. I. 1971 – Zakonomernosti mikrobiotičeskogo raspredelenija *Collembola* v svjazi s dinamikoj rastitelnogo pokrova v pjatnistoj tundre Tajmyra – *Zool. Ž.* 50: 817–823.
4. Böckemühl J. 1956 – Die Apterygoten des Spitzberges bei Tübingen, eine faunistisch-ökologische Untersuchung – *Zool. Jb. (Syst.)*, 84: 113–194.
5. Černova N. M. 1970 – Gesetzmässigkeiten der Verteilung von Mikroarthropoden im Komposthaufen – *Pedobiologia*, 10: 365–372.
6. Černova N. M., Čugunova M. N. 1967 – Analiz prostranstvennogo raspredelenija počvoobitajuščich mikroartropod v predelach odnoj rastitelnoj asociacii – *Pedobiologia*, 7: 67–87.
7. Choudhuri D. K., Roy S. 1967 – Quantitative composition of the collembolan fauna of some uncultivated fields in Nadia district (West Bengal) with a correlation between monthly population and individual soil factor – *Rev. Ecol. Biol. Sol.*, 4: 507–515.
8. Christiansen K. 1967 – Competition between collembolan species in culture jars – *Rev. Ecol. Biol. Sol.*, 4: 439–462.
9. Davis B. N. K. 1963 – A study of micro-arthropod communities in mineral soil near Corby, Nothants – *J. Anim. Ecol.* 32: 49–71.
10. Debauche H. R. 1962 – The structural analysis of animal communities of the soil (In: *Progress in soil zoology*. Ed. P. W. Murphy) – Butterworth's, London, 10–25.
11. Dice L. R. 1945 – Measures of the amount of ecological association between species – *Ecology*, 26: 297–302.
12. Dowdy W. W. 1965 – Studies on the ecology of mites and *Collembola* – *Am. Midl. Nat.* 74: 196–210.
13. Edwards C. A., Fletcher K. E. 1971 – A comparison of extraction methods for terrestrial arthropods (In: *Methods of study in quantitative soil ecology: population, production and energy flow*. Ed. J. Phillipson. IBP Handbook No. 18) – Blackwell Scientific Publications, Oxford, Edinburgh, 150–185.

14. Edwards C. A., Loftly J. R. 1971 – The influence of temperature on numbers of invertebrates in soil, especially those affecting primary production (In: IV colloquium pedobiologiae, Dijon, 1970) – INRA, Annale de Zool.-Ecol. animale. Paris, 71–77.
15. Forbes S. A. 1907 – On the local distribution of certain Illinois fishes. An essay in statistical ecology – Bull. Ill. St. Lab. nat. Hist. 7: 273–303.
16. Gisin G. 1952 – Ökologische Studien über die Collembolen Blattkomposts – Revue suisse Zool. 59: 543–578.
17. Gisin H. 1943 – Ökologie und Lebensgemeinschaften der Collembolen in schweizerischen Exkursionsgebiet Basels – Revue suisse Zool. 50: 131–224.
18. Gisin H. 1957 – Collembolen einiger Waldböden des Fuorngebietes (Schweizerischer Nationalpark) – Ergebn. wiss. Unters. schweiz. NatnParcs, 6 (N. F.): 109–114.
19. Glasgow J. P. 1939 – A population study of subterranean soil *Collembola* – J. Anim. Ecol. 8: 323–353.
20. Haber A. 1957 – Badania nad rolą płazów w biocenozach lasów objętych gradacją szkodników i akcjami chemicznymi w latach 1948–1949 – Rocz. Nauk. leśn. 20: 1–90.
21. Hairston N. G. 1959 – Species abundance and community organization – Ecology, 40: 404–416.
22. Hale W. G. 1966 – A population study of moorland *Collembola* – Pedobiologia, 6: 65–99.
23. Hammer M. 1944 – Studies on the oribatids and collemboles in Greenland – Meddr Grønland, 141: 1–210.
24. Hughes R. D. 1962 – The study of aggregated populations (In: Progress in soil zoology. Ed. P. W. Murphy) – Butterworth's, London, 51–55.
25. Jahn E. 1950 – Bodentieruntersuchungen in den Flugsandgebieten des Marchfeldes – Z. angew. Ent. 32: 208–274.
26. Joosse E. N. G. 1969 – Population structure of some surface dwelling *Collembola* in coniferous forest soil – Neth. J. Zool. 19: 621–634.
27. Joosse E. N. G. 1970 – The formation and biological significance of aggregations in the distribution of *Collembola* – Neth. J. Zool. 20: 299–314.
28. Joosse E. N. G. 1971 – Ecological aspects of aggregation in *Collembola* – Rev. Ecol. Biol. Sol, 8: 91–97.
29. Kaczmarek M. 1960 – Próba zastosowania metody pułapkowej do badań *Collembola* – Ekol. pol. B, 6: 323–331.
30. Kaczmarek M. 1963 – Jahreszeitliche Quantitätsschwankungen der Collembolen verschiedener Waldbiotope der Puszca Kampinowska – Ekol. pol. A, 11: 127–139.
31. Kaczmarek M. 1973 – *Collembola* in the biotopes of the Kampinos National Park distinguished according to the natural succession – Pedobiologia, 13: 257–272.
32. Kaczmarek W. 1953 – Badania nad zespołami mrówek leśnych – Ekol. pol. 1: 69–96.
33. Kaczmarek W. 1960 – Z badań nad strukturą przestrzenną populacji kilku wybranych gatunków *Collembola* – Ekol. pol. A, 8: 49–64.
34. Kajak A. 1957 – O zakresie stosowania wskaźnika współwystępowania – Ekol. pol. B, 3: 131–134.
35. Król S. 1952 – Rezultaty badań nad mikrofauną gleby w borach sosnowych – Biul. Centr. Inst. Roln. 2(4): 78–79.
36. Kühnelt W. 1950 – Bodenbiologie – Verlag Herold, Wien, 368 pp.
37. Macfadyen A. 1952 – The small arthropods of *Mollina fen* at Cothill – J. Anim. Ecol. 21: 87–117.
38. Margowski Z. 1952 – Bezkręgową fauną gleb leśnych w drzewostanach bukowych i sosnowych nadleśnictwa Sierzno – Biul. Centr. Inst. Roln. 2(4): 81–83.
39. Margowski Z., Prusinkiewicz Z. 1955 – Wpływ czynników ekologicznych na występowanie i działalność życiową drobnej fauny glebowej – Pozn. Tow. Przyjaciół Nauki, Wydz. Mat.-Przyr. 16: 1–31.
40. McMillan J. H. 1969 – The ecology of acarina and collembolan fauna of two New Zealand pastures – Pedobiologia, 9: 372–404.
41. Milne S. 1962 – Phenology of a natural population of soil *Collembola* – Pedobiologia, 2: 41–52.
42. Perel T. 1964 – Kompleksy počvennych bezpozvonočnych v nekotorych tipach lesa serebrjanoborskogo opytnogo lesničestva (In: Stacionarnye biogeocenotičeskie issledovanija v južnoj podzone tajgi. Ed. V. N. Sukačev) – Izdatel'stvo "Nauka", Moskva, 183–194.

43. Petersen H. 1971 – Parthenogenesis in two common species of *Collembola*: *Tullbergia krausbaueri* (Bömer) and *Isotoma notabilis* Schäffer – Rev. Ecol. Biol. Sol, 8: 133–138.
44. Poole T. B. 1961 – An ecological study of the *Collembola* in a coniferous forest soil – Pedobiologia, 1: 113–137.
45. Poole T. B. 1964 – A study of the distribution of soil *Collembola* in three small areas in coniferous woodland – Pedobiologia, 4: 35–42.
46. Rapoport E. H., Tschapek M. 1967 – Soil water and soil fauna – Rev. Ecol. Biol. Sol, 4: 1–58.
47. Schaller F. 1949 – Zur Ökologie der Collembolen in Kalksteinboden – Zool. Jb. (Syst.), 78: 263–293.
48. Sheals J. G. 1957 – The *Collembola* and *Acarina* of uncultivated soil – J. Anim. Ecol. 26: 125–134.
49. Stach J. 1947 – The apterygotan fauna of Poland in relation to the world-fauna of this group of insects. Family: *Isotomidae* – Acta monogr. Mus. Hist. Nat. Kraków, 488 pp.
50. Stach J. 1949a – The apterygotan fauna of Poland in relation to the world-fauna of this group of insects. Families: *Neogastruridae* and *Brachystomellidae* – Acta monogr. Mus. Hist. Nat. Kraków, 341 pp.
51. Stach J. 1949b – The apterygotan fauna of Poland in relation to the world-fauna of this group of insects. Families: *Anuridae* and *Pseudachorutidae* – Acta monogr. Mus. Hist. Nat. Kraków, 122 pp.
52. Stach J. 1951 – The apterygotan fauna of Poland in relation to the world-fauna of this group of insects. Family: *Bilobidae* – Acta monogr. Mus. Hist. Nat. Kraków, 197 pp.
53. Stach J. 1954 – The apterygotan fauna of Poland in relation to the world-fauna of this group of insects. Family: *Onychiuridae* – PWN, Kraków, 219 pp.
54. Stach J. 1956 – The apterygotan fauna of Poland in relation to the world-fauna of this group of insects. Family: *Sminthuridae* – PWN, Kraków, 287 pp.
55. Stach J. 1957 – The apterygotan fauna of Poland in relation to the world-fauna of this group of insects. Families: *Néelidae* and *Dicyrtomidae* – PWN, Kraków, 113 pp.
56. Stach J. 1960 – The apterygotan fauna of Poland in relation to the world-fauna of this group of insects. Tribe: *Orchesellini* – PWN, Kraków, 151 pp.
57. Stach J. 1963 – The apterygotan fauna of Poland in relation to the world-fauna of this group of insects. Tribe: *Entomobryini* – PWN, Kraków, 126 pp.
58. Stevanovič D. 1956 – *Collembola* populations in the forest associations of Kopaonik – Zborn. Rad. Kniga, 7: 1–16.
59. Strenzke K. 1949 – Ökologische Studien über die Collembolagesellschaften feuchten Böden Ost-Holsteins – Arch. Hydrobiol. 42: 201–303.
60. Tarwid K. 1960 – Szacowanie zbieżności nisz ekologicznych gatunków drogą oceny prawdopodobieństwa spotkania się ich w połowach – Ekol. pol. B, 6: 115–130.
61. Traczyk H., Traczyk T. 1965 – Charakterystyka fitosocjologiczna terenów badawczych Zakładu Ekologii PAN w Dziekanowie Leśnym (Puszcza Kampinoska) – Fragm. Faun. Geobot. 11: 547–562.
62. Usher M. B. 1969 – Some properties of the aggregations of soil arthropods: *Collembola* – J. Anim. Ecol. 38: 607–622.
63. Vander Drift J. 1951 – Analysis of the animal community in a beech forest floor – Tijdschr. Ent. 94: 1–168.
64. Vannier G. 1970 – Reactions des microarthropodes aux variations de l'état hydrique du sol – Centre Nation. Rech. Scient. Paris, 25–258.
65. Vannier G. 1971 – Importance du point d'hygroscopie maximale dans une analyse factorielle du biotope des Collembolés – Rev. Ecol. Biol. Sol, 8: 81–90.
66. Volz P. 1934 – Untersuchungen über die Mikroschichtung der Fauna von Waldböden – Zool. Jb. (Syst.), 66: 153–210.
67. Volz P. 1954 – Über die Rolle der Tierwelt in Waldböden besonders beim Abbau der Fallstreu – Z. PflErnähr. Düng. Bodenk. 64: 230–237.
68. Wasilewski A. 1967 – The effect of interspecific competition on the number and distribution of birds in forest biotopes – Ekol. pol. A, 15: 641–695.

69. Weis - Fogh T. 1948 - Ecological investigations on mites and *Collembola* in the soil - *Natura* jutr. 1: 137-270.
70. Wink U. 1969 - Die Collembolen und Oribatiden Populationen einiger saurer Auböden Bayerns in Abhängigkeit von der Bodenfeuchtigkeit - *Z. angew. Ent.* 64: 121-136.

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