KOMITET EKOLOGICZNY - POLSKA AKADEMIA NAUK

EKOLOGIA POLSKA — SERIA A

Tom XIV Warszawa 1966 Nr 15

Jadwiga ŁUCZAK

THE DISTRIBUTION OF WANDERING SPIDERS IN DIFFERENT LAYERS OF THE ENVIRONMENT AS A RESULT OF INTERSPECIES COMPETITION*

The distribution of wandering spiders in the field-layer and pines of the young pine forests was analysed. Comparing the distribution of separate species in each of the forest layers with its percentage share in the field spiders association and the pine spiders association at several stands it was stated that some species show a correlation of these elements which, it is believed, is a result of the interspecies competition of spiders. The type of correlation depends on the importance of the species in the association.

INTRODUCTION AND METHOD

In August and September 1959 the spiders from the field-layer (heather) and shrub-layer (young pines) of the eight young pine forests of the Kampinos Forest's edge at Dziekanów Leśny were analysed. The detailed characterization of the stands is given in Łuczak's work (1963) in which the web spiders associations were analysed. The stands differ mainly in the pines age: we can discern the oldest stand *A* (age 11–16 years); *B*, *C* and *D* belonging to the group of older stands (up to 13 years) and *E*, *F*, *G* and *H* – belonging to the group of younger stands (up to 10 years). All of them are on the dune areas of the Kampinos Forest in which xerophilous and thermophilous fauna and flora are to be found.

The heather spiders were collected with a sweep-net; the material from 25 sweeps of the sweep-net formed one sample; up to ten samples were taken from each of the stands on the day of collecting them. During the two months

*From the Institute of Ecology Polish Academy of Sciences, Warszawa.

period five series (5 times 10) of such samples were collected from each of the stands; all in all the material from 400 sweep-net samples (i.e. 2, 751 spiders) was collected. From the pines they were gathered by shaking down to a sweep-net bag; for one sample from one stand spiders from 50 young pines (3 branches each) were shaken down and together the material from 5 such samples (at each stand) was collected. All in all spiders were collected from 2, 000 pines (1, 280 spiders).

Structure of domination of wandering spiders on heather

Tab. I

Species	Stands							
	A	*B*	*C*	*D*	*E*	*F*	*G*	*H*
	per cent							
Oxyopes ramosus	40	46	53	57	40	37	45	23
Xysticus cristatus	3.4	5.3	3.4	10	2.8	6.9	6.4	8.3
Philodromus aureolus	9.4	16	7.1	6.5	7	14.7	2.9	7.3
Philaeus chrysops	0.3	0.3	0.3	1.1	9	9.8	2.1	8
Clubiona trivialis	6.6	2.8	6	4.2	1.1	0.6	1.6	2.3
Evarcha arcuata	8.1	4.4	6.2	2.5	0.8	0.3	1.1	1.3
Philodromus emarginatus	0.6	0.3	0	0.4	0.5	0.3	0.5	2.3

Structure of domination of wandering spiders (on young pines)

Tab. II

Species	Stands							
	A	*B*	*C*	*D*	*E*	*F*	*G*	*H*
	per cent							
Oxyopes ramosus	30	38	40	53.6	25.8	25	24.5	7.5
Xysticus cristatus	6	4.1	7	2.7	1.6	7.1	7	8.2
Philodromus aureolus	14	30	30	24.8	17.5	25	18.5	21.8
Philaeus chrysops	0	2.3	1.2	0.5	11.5	7.7	4.6	9
Clubiona trivialis	6	6	11	0.5	3.8	8	4.6	11.2
Evarcha arcuata	1.4	0	0.6	0.5	0	0	0	0
Philodromus emarginatus	7.5	2.9	3.8	7	10	7.1	17.8	4.5

The domination structure of wandering spiders was compared, i.e. the percentage share of the component species in the whole association of spiders from the heather and pines respectively (Tab. I, II). The index of distribution of individual species (α) was used. It was calculated by dividing the figure indicating the number of the given species on the pines (N_s) by the figure stating its number in the heather (N_r) (Tab. III).

$$\alpha = \frac{N_s}{N_r}.$$

The higher the index, the more individuals of this species are to be found in the pine-layer.

In the present paper the distribution of the wandering spiders in the two layers of the environment is analysed in a detailed way and the possible ecological reasons of this distribution are set out.

From the so far published works on distribution of spiders in different layers of the environment it is evident that communities of heather spiders and shrub spiders cannot be definitely separated from each other; numerous species are able to wander from one layer to the other.

Bristowe (1929) and Knülle (1953) state that distribution of the species of spiders depends of physical features of the plants, for example their height and morphology. Tretzel (1952) and Vité (1953) stress the importance of the size of spiders (small ones live in the litter, larger ones in the higher layers) but it is true only in a very broad sense and with many exceptions. Łuczak (1959) states that the field-layer is the habitat of many spiders in early growth stages which in their mature phase live in other layers and even, exceptionally, in a different environment. Charitonov (1953) and Vité (1953) think that one of the main reasons for any migration of spiders to the adjacent layers is searching for food. Numerous arachnologists (among others Rabeler 1957 and Łuczak 1960) noticed that the community of the litter is very distinctly different specifically from other communities while the differences between the communities of the field- and shrub-layers spiders are not so distinct (though still easily discernible).

Turnbull (1960) and Łuczak (1960) stated on the grounds of their research into the distribution of spiders in oak and pine forest that many species, in spite of the fact that they are distributed in two different layers, are much more numerous in one of them.

Turnbull states that spiders have a strong tendency to a layer distribution in the vertical structural forest strata although this tendency may be somewhat blurred by seasonal and diel periodicities of spiders; though many species show a clear preference to one of the layers in which they usually live, nonetheless they have a tendency to penetrate the adjacent layers.

Łuczak proves that the percentage of species which individuals were distributed evenly in the field- and shrub-layers is insignificant. The abundant species whose individuals can be found in both these layers live predominantly in only one of them.

The data given above testify that the phenomenon of stratification can be conditioned by different factors. But we must clearly spell out the two aspects of this problem: the division of species into those which live in various layers and the division of population of the same species into parts which are found in the two layers. The first phenomenon is caused by a group of features which could in general be called physio-biological adaptations to life in the given layer, the other by a group of ecological features (actual response to climatic, weather, biotic, etc. factors). In the present paper we

are interested only in this second aspect of the stratification of spiders. The index of distribution of a species (α) from different stands gives information about the degrees of occupation of both these layers by the population of this species.

RELATION BETWEEN THE INDEX OF DOMINATION AND THE INDEX OF DISTRIBUTION

The analysis of the material has shown that some species from the group which are able to distribute itself on both the pines and in the field-layer mostly tend to be in one layer only. With those species which are mainly found in the field-layer the index of distribution α is low (< 1), and those living on pines relatively high (generally > 5) (Tab. III). With other species the index of distribution is very variable (different at different stands).

Index of distribution of wandering spiders

$$\alpha = \frac{N_s}{N_r}$$

Tab. III

Species	Stands							
	A	*B*	*C*	*D*	*E*	*F*	*G*	*H*
Oxyopes ramosus	0.34	0.45	0.38	0.38	0.33	0.28	0.22	0.14
Xysticus cristatus	0.82	0.41	1.00	0.11	0.30	0.50	0.46	0.44
Philodromus aureolus	0.70	1.02	2.09	1.55	1.28	0.74	2.55	1.32
Philaeus chrysops	0	4	2	0.25	0.62	0.27	0.88	0.50
Clubiona trivialis	0.43	1.44	0.95	0.05	1.75	6.50	1.17	2.14
Evarcha arcuata	0.08	0	0.05	0.09	0	0	0	0
Philodromus emarginatus	5.50	5		6	9.50	11	13.50	0.86

At the same time the index of percentage share of the field and pine species of spiders in the associations of both the layers is also variable with these species. The comparison of these figures indicates the existence of certain correlation between the changes of the two indices. It enables us to form a hypothesis about the correlation between the two ecological phenomena: the rate of domination in the association and the rate of distribution of the species in the two layers. This hypothesis based on the well-known ecological fact that some species of spiders penetrate the adjacent layers, says that the structure of domination of wandering spiders in the analysed environment formation: heather – pines, is the result of competition between species of spiders.

If this is true then we can expect theoretically that the analysed species will show three types of regular changes in the calculated numeral indices (share in the association of pine spiders, share in the association of the field spiders and the index of distribution).

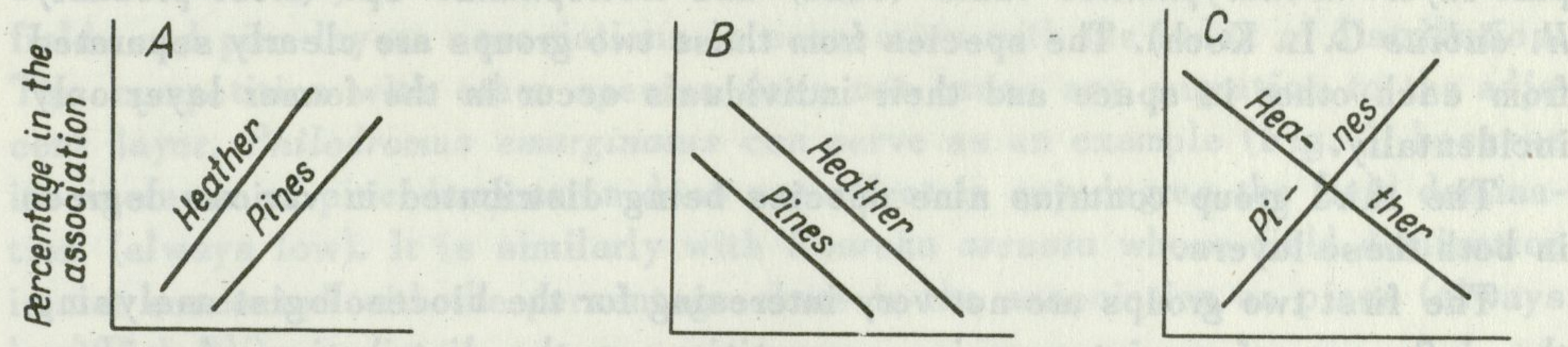

Fig. 1. Scheme of three types of regular changes in the indices. Explanations in text

It is shown schematically in Figure 1.

1. Scheme *A* presents regular changes of the three above mentioned indices concerning the "strong" species, winning the competition with other species in each of these layers. The species living in, for exemple, the field-layer as its share in the association grows, shifts more and more to the pines where it also increases the degree of domination in the association of spiders.

2. Scheme *B* presents changes of the indices concerning the "weak" species losing its competition with other species. The species reduces numerically in the field-layer crossing more and more to the pines; but its domination there also decreases under pressure from the other species of the association.

3. Scheme *C* presents the species displaying "ability for compensation" in the utilization of the layers of the environment. Under the conditions enabling it to maintain considerable population (e.g. in the field-layer), it lives there crossing only insignificantly to the pines. As its domination in the field-layer decreases, it crosses to the pines increasing its share in the association of this habitat. Losing the competition in the field-layer it wins in the association of pine spiders.

RESULTS

In all, 33 species of wandering spiders were collected. In the present paper we are particularly interested in the species occurring at all or the majority of the stands (16 species).

The 16 species of wandering spinders collected in the young pine forests can be divided into three groups; the species belonging to these groups distribute themselves in the analysed environment in a different way. The species connected in this particular environment almost exclusively with the field-layer belong to the first group. They are: *Philodromus histrio* (Latr.), *Tibellus* sp., *Misumena vatia* (Clerck), *Evarcha falcata* (Clerck), *Pisuara mirabilis* (Clerck). The second group contains the species connected almost exclusively with the

pine-layer: *Dendryphantes rudis* (Sund) and *Heliophanus* sp. (most probably *H. dubius* C.L. Koch). The species from these two groups are clearly separated from each other in space and their individuals occur in the former layer only incidentally.

The third group contains nine species being distributed in various degrees in both these layers.

The first two groups are not very interesing for the biocenologist analysing the influence of an interspecies competition on the distribution of spiders in the two layers of the environment. But the third group is very interesting because of the phenomenon of a variable intensity of migration into the adjacent layers. Only the species of the third group will be discussed, of course, as integral elements of wandering spiders associations of each of the layers of the forest vegetation.

Among the species of this group we can discern various degrees of connections with one of the layers. As the above described index of distribution shows (Tab. III) *Evarcha arcuata* (Clerck) is most strongly combined with the field-layer, while *Philodromus emarginatus* (Schrank) with the pine-layer. The data given by Locket and Millidge (1951) confirm the preferences of these species. The distribution of the rest of the species – *Oxyopes ramosus* (Panz.), *Xysticus cristatus* (Clerck), *Philodromus aureolus* (Clerck), *Philaeus chrysops* (Poda), *Clubiona trivialis* C.L. Koch, *Tmarus piger* (Walck) and *Cheiracanthium* sp. testifies to a greater possibility of life in both these layers and is conditioned, as far as we can judge, both by the pressure of an interspecies competition and the species population expansiveness. *Oxyopes ramosus* and *Clubiona trivialis* are treated by arachnologists as occurring more readily on lower plants (the field-layer), *Xysticus cristatus* as a species found in each of the layers in the same degree, *Philodromus aureolus* as a species occurring mainly on shrubs.

As many arachnologic works show (and particularly Turnbull 1960) the field-layer is the habitat where different spider species from different layers of the forest vegetation can encounter. It is characterised by the greater number of spiders than in other layers (with the only exception of the litter of some forests). These features of the field-layer may cause the occurrence of the competition between the species having similar ecological requirements for the place where they live or for the possibilities of getting their prey. The pressure of competition forces a part of the population of different species to migrate to shrubs and small trees growing in this environment.

We shall discuss in a more detailed way the distribution of the species of the third group comparing the value of its index of distribution with the value of domination in the wandering spiders association of the field- and pine-layers (Figs. 2–9) and with the given schemes (Fig. 1). Two species, *Tmarus piger* and *Cheiracanthium* sp., are excluded from the analysis because of their insignificant numben.

Species with a relatively strong ecological preference to one of the layers

do not show any correlation in the changes of the rate of domination in the field- and pine-layers associations in connection with the index of distribution. The competition with other species does not cause any migration to the adjacent layer. *Philodromus emarginatus* can serve as an example (Fig. 2) because its increase of pine domination does not affect in any degree the field domination (always low). It is similarly with *Evarcha arcuata* whose field domination is not connected with the percentage share in the association on pines (always low)(Tab. IV).

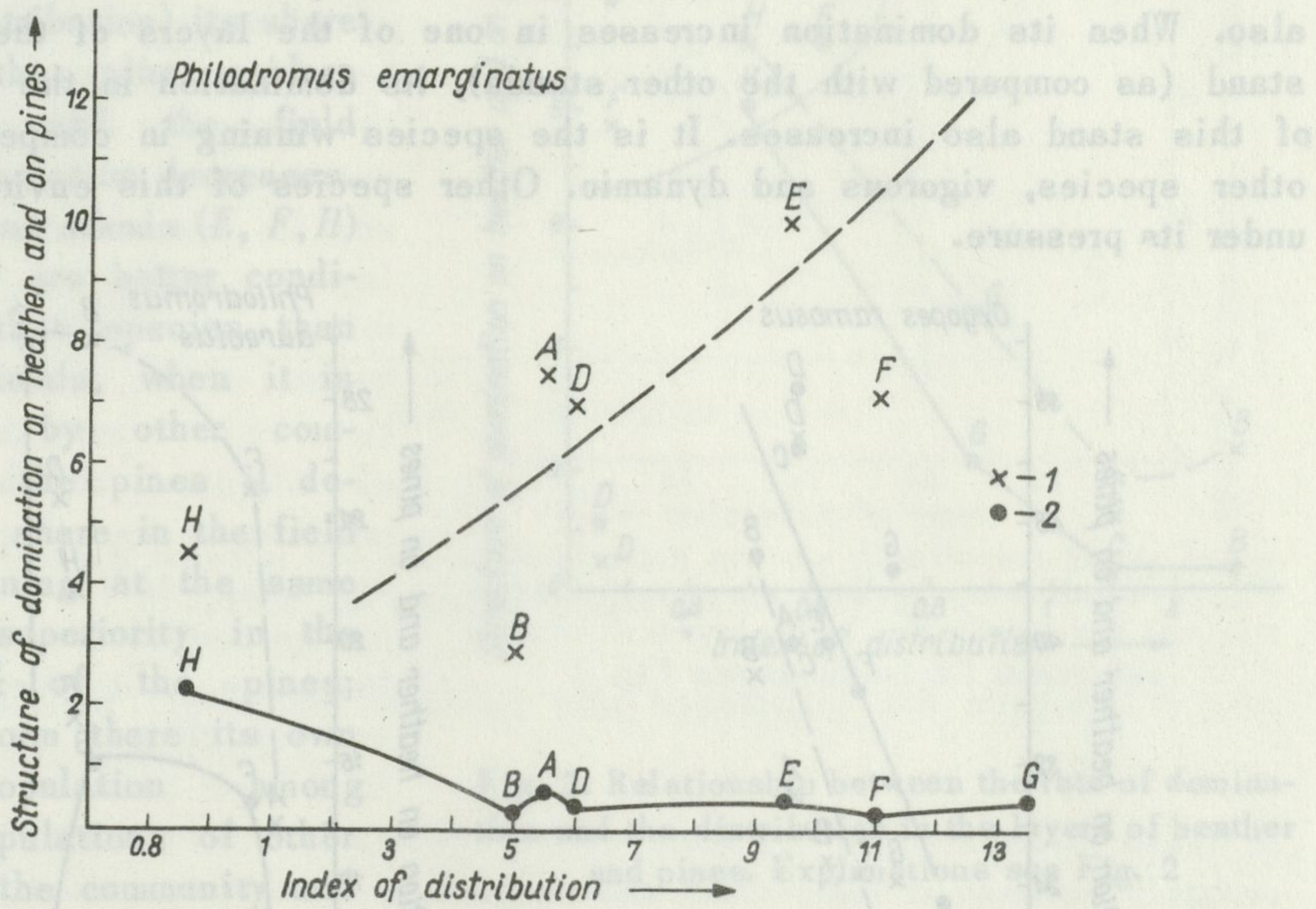

Fig. 2. Relationship between the rate of domination and the distribution in the layers of heather and pines

1 – **pines,** *2* – **heather. Letters determine particular stands**

Number of *Evarcha arcuata* on heather and on pines

Tab. IV

Layers	Stands							
	A	*B*	*C*	*D*	*E*	*F*	*G*	*H*
Heather	26	14	20	11	3	1	4	4
Pines	2	0	1	1	0	0	0	0

The remaining species show the connection between the rate of domination in each of the layers and the index of distribution which is understandable in the light of the above presented hypothesis about the interspecies competition of spiders. One can find among them instances of ecological situations presented schematically in Figure 1.

Oxyopes ramosus is a dominant species in the examined associations of wandering spiders. Its percentage share oscillates between 23 and 57% for heather and between 7.5 and 53% for pines. In another paper (Łuczak 1960) the author showed that this species was dominant in the community of heather spiders from the young pine forest and represented there from 24 to 42% of the number of all spiders. It represents the dependence of the first type between the distribution and domination in each of the layers (Fig. 3, cf. Fig. 1 *A*). As the number of individuals on the pines increases, both its domination in this layer and its share in the heather spiders association increase also. When its domination increases in one of the layers of the particular stand (as compared with the other stands), its domination in the other layer of this stand also increases. It is the species winning in competition with other species, vigorous and dynamic. Other species of this environment are under its pressure.

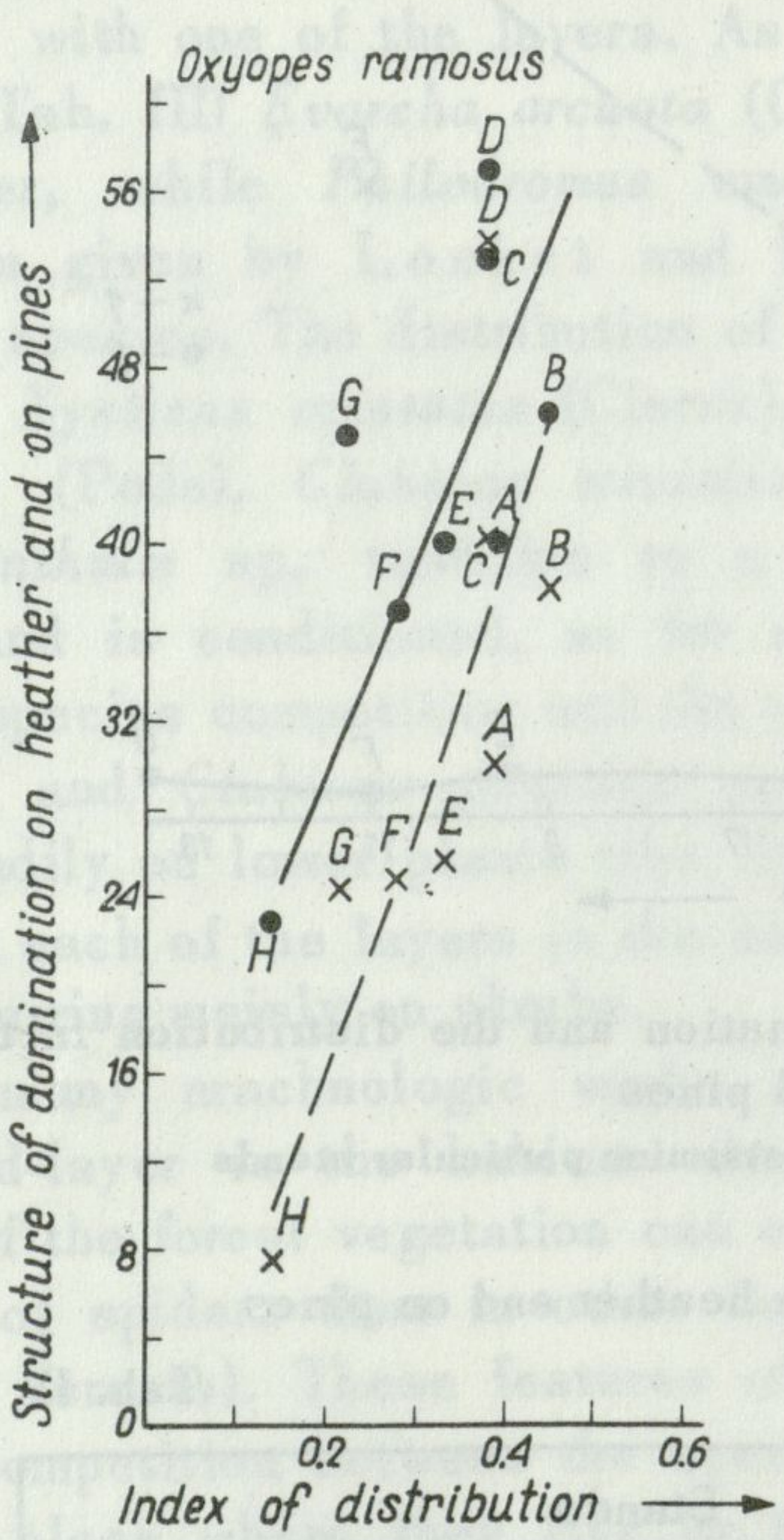

Fig. 3. Relationship between the rate of domination and the distribution in the layers of heather and pines. Explanations see Fig. 2

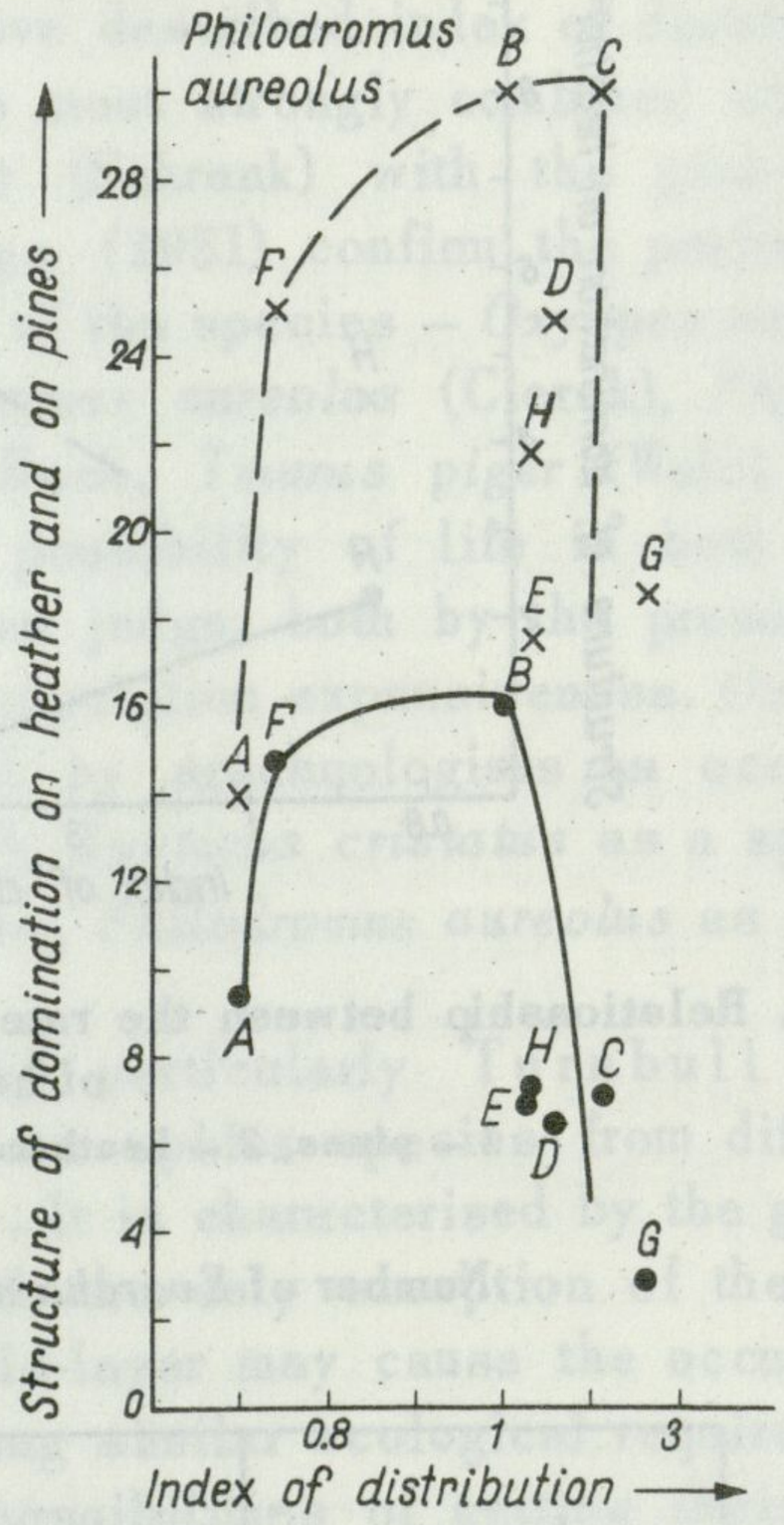

Fig. 4. Relationship between the rate of domination and the distribution in the layers of heather and pines. Explanations see Fig. 2

Philodromus aureolus behaves similarly but not at all the stands: when the size of its population on the pines corresponds to the value of the index of distribution > 1 (i.e. when the pines are more numerously habitated) its share in the field-layer association sharply decreases. It may indicate that

from some point of population density it encounters the resistance of other species unabling it to increase its share in the association (Fig. 4, cf. Fig. 1 *A*).

Another dependence between the distribution and domination is presented by the species *Philaeus chrysops*, rather rare in Poland (Fig. 5, cf. Fig. 1 *B*). When it crosses intensively to the pines (as calculated by the index of distribution) its share both in the pine spiders association and the field spiders association decreases. At some young stands (*E*, *F*, *H*) where there are better conditions for that species than at older stands, when it is "expelled" by other competitors to the pines it decreases its share in the field without gaining at the same time any superiority in the environment of the pines; it cannot form there its own strong population among stronger populations of other species of the community and its percentage share decreases.

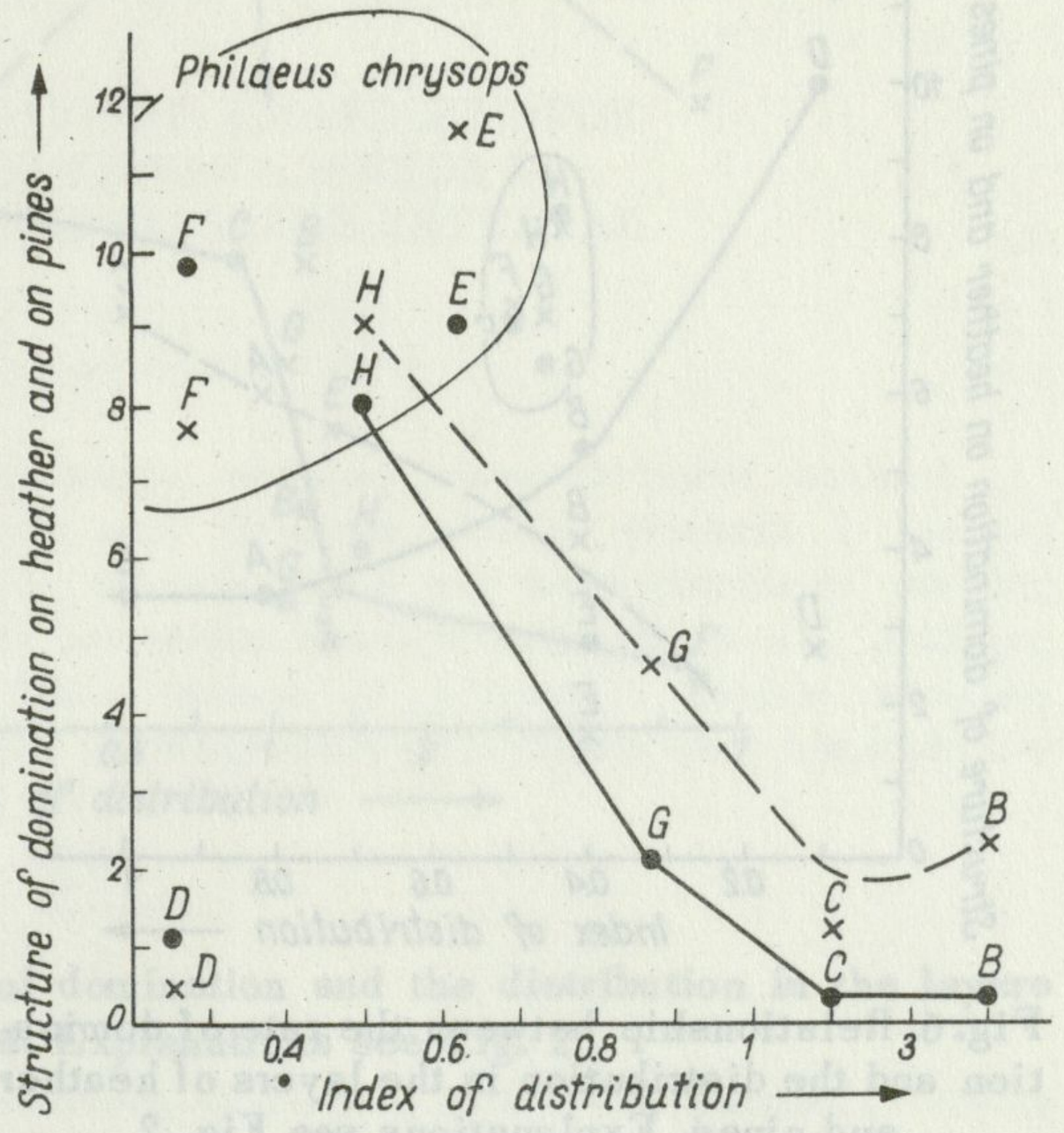

Fig. 5. Relationship between the rate of domination and the distribution in the layers of heather and pines. Explanations see Fig. 2

It is an instance of a "weak" species losing in the competition with other species always when the conditions of the environment differ from the optimal conditions for this species. And even when the best conditions occur the populations of this species are not large and do not exceed 11.5% of the association. It is a species highly specialized in its environmental requirements, in Poland on the northern frontiers of its range. This is a probable cause why it cannot form a strong, stable population, especially in slightly worse conditions of shadier and wetter older stands.

Still another dependence is shown by *Xysticus cristatus* (Fig. 6, cf. Fig. 1 *C*). This species presents the case of an increase of the rate of domination on pines with its simultaneous decrease in the field-layer. There are stands which have rather strong population of this spider (larger percentage share in the association) in the heather; there it has no tendency to shift to the pines. If however because of the competition some part of the population is "pushed up" to the branches of the pines, the share of the species in the field-layer decreases. On the pines with "sparser" spider populations

(larger volume of the layer) it may encounter not so strong a competition and then increases its share in the association. It should be stressed that such conditions occur at older stands. At the three youngest (*F*, *G* and *H*) the analysed dependence is not regular.

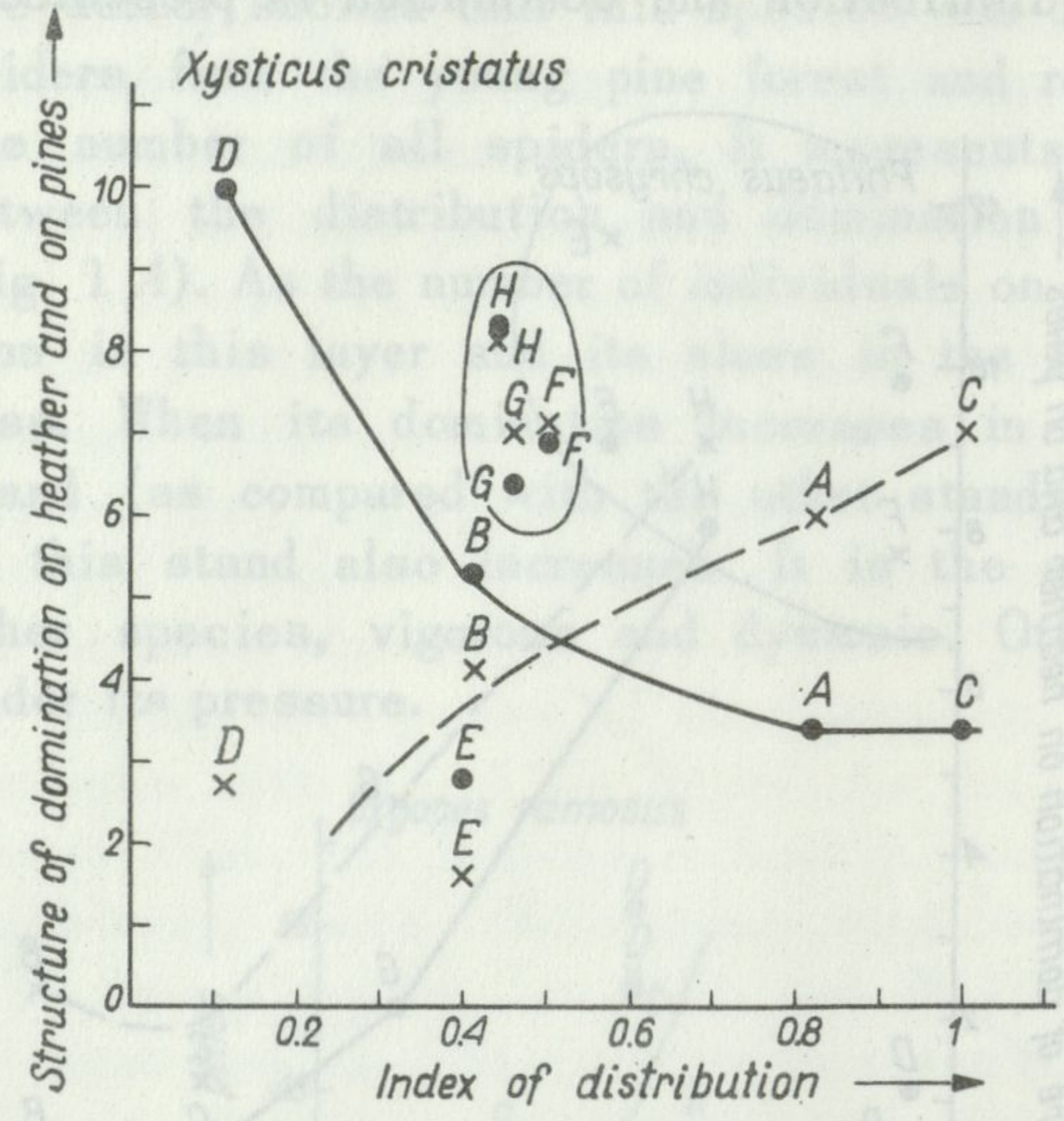

Fig. 6. Relationship between the rate of domination and the distribution in the layers of heather and pines. Explanations see Fig. 2

Clubiona trivialis behaves similarly at the three oldest stands (*A*, *C* and *D* – Fig. 7 cf. Fig. 1 *C*). The more the population shifts to the pines, the more the domination of the species on the pines increases and its domination in the field-layer decreases. But this relation is valid only at smaller values of the index of distribution, i.e. when the intensity of migration to the pines is smaller; at the values from $\alpha = 1$ upwards, that is when the occupation of the pines is more intensive, the domination decreases sharply not only in the field-layer but also on the pines. In these circumstances the share of the species in the association decreases, probably because it encounters the resistance of the competing species. We can describe such species as "able for compensation" in the utilization of various layers of the environment under conditions of competition.

The existence of different ecological types of populations in the association of similar life forms does not require any justification and is a well known fact. In all of them we can find dominant forms which belong to "prosperous" and dynamic species and forms constituting average and small populations. But only the analysis of the process of distribution in the two layers of the environment together with the analysis of the phenomenon of domination in the associations gives us a broader basis to support the hypothesis about the interspecies competition in the association and its ecological effects. Many ecologists take the structure of domination as a result of an interspecies competition against the background of changeable and favouring, sometimes one species and sometimes another species, conditions of the environment.

In the paper about the web spiders from the same young pine forests (Łuczak 1963) the author put forward the same hypothesis concerning the ecological association. On the material of wandering spiders from the

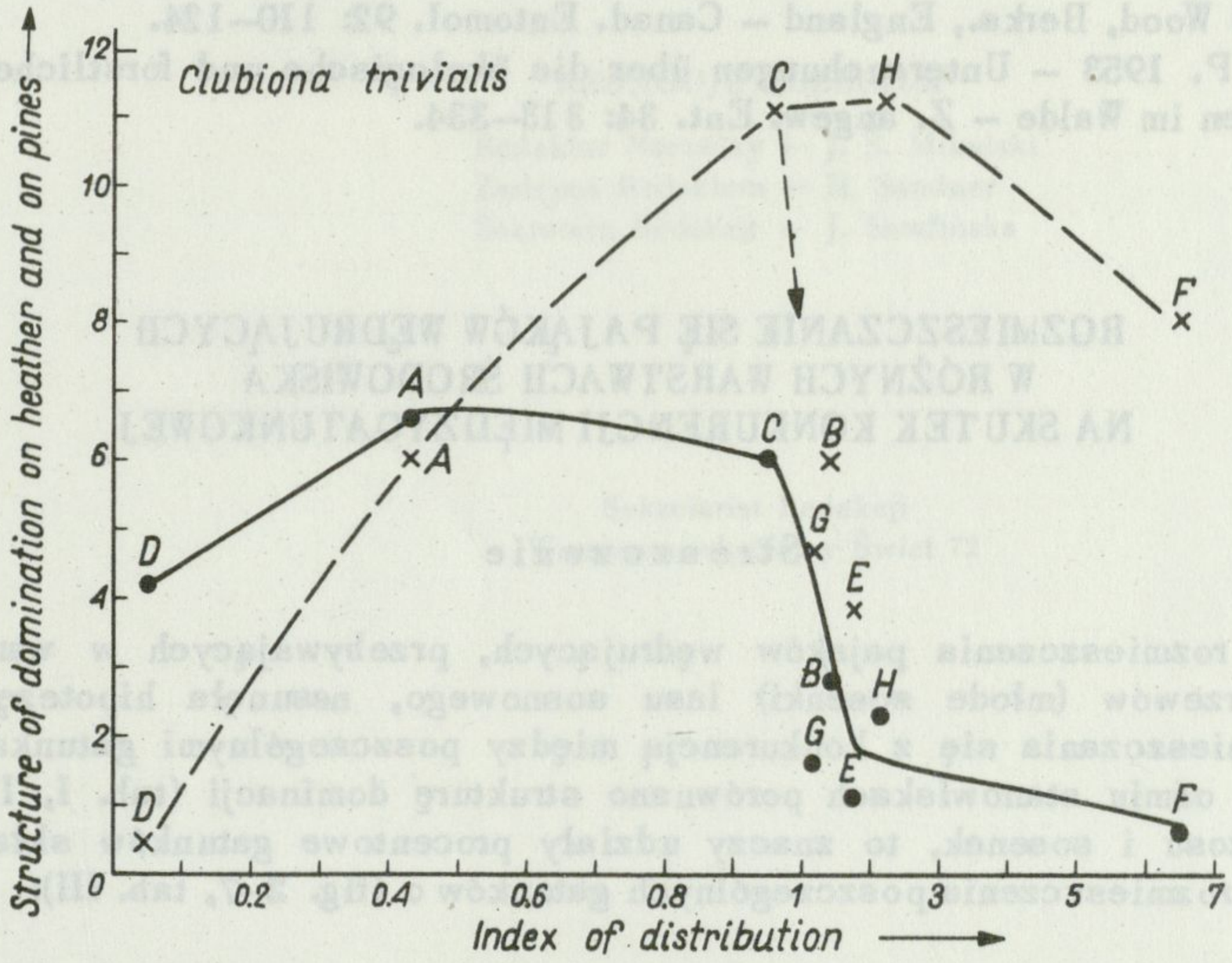

Fig. 7. Relationship between the rate of domination and the distribution in the layers of heather and pines. Explanations see Fig. 2

same environment the author confirms this hypothesis and supports it with some additional arguments.

REFERENCES

1. Bristowe, W.S. 1929 – The distribution and dispersal of spiders – Proc. zool. Soc. London, 4: 633–657.
2. Charitonov, D.E. 1953 – Paukoobraznye – *Arachnoidea*, Pauki-*Araneina* (Životnyj Mir SSR, v. 4) – Moskva: 556–565.
3. Knülle, W. 1953 – Zur Ökologie der Spinnen an Ufern und Küsten – Z. Morphol. Ökol. 42: 117–158.
4. Locket, G.H. and Millidge, A.F. 1951 – British spiders, v. I – London, 310 pp.
5. Łuczak, J. 1959 – The community of spiders of the ground flora of pine forest – Ekol. Pol. A, 7: 285–315.
6. Łuczak, J. 1960 – Rozmieszczenie piętrowe pająków w lesie – Ekol. Pol. B, 7: 39–50.
7. Łuczak, J. 1963 – Differences in the structure of communities of web spiders in one type of environment (young pine forest) – Ekol. Pol. A, 11: 159–221.
8. Rabeler, W. 1957 – Die Tiergesellschaften eines Eichen-Birkenwaldes im Nordwestdeutschen Altmoränengebiet – Mitt. flor-soziol. Arbeitsgemeinsch. N. F. H. 6/7.
9. Tretzel, E. 1952 – Zur Ökologie der Spinnen (*Araneae*). Autökologie der Arten in Raum von Erlangen – Sitzungsber. phys.-med. Soc. Erlangen, 75: 1–131.

10. Turnbull, A.L. 1960 – The spider population of a stand of oak (*Quercus robur* L.) in Wytham Wood, Berks., England – Canad. Entomol. 92: 110–124.
11. Vité, J.P. 1953 – Untersuchungen über die ökologische und forstliche Bedeutung der Spinnen im Walde – Z. angew. Ent. 34: 313–334.

ROZMIESZCZANIE SIĘ PAJĄKÓW WĘDRUJĄCYCH W RÓŻNYCH WARSTWACH ŚRODOWISKA NA SKUTEK KONKURENCJI MIĘDZYGATUNKOWEJ

Streszczenie

Analiza rozmieszczenia pająków wędrujących, przebywających w warstwie runa (wrzos) i krzewów (młode sosenki) lasu sosnowego, nasunęła hipotezę związania procesu rozmieszczania się z konkurencją między poszczególnymi gatunkami zespołu pająków. Na ośmiu stanowiskach porównano strukturę dominacji (tab. I, II) zespołów pająków wrzosu i sosenek, to znaczy udziały procentowe gatunków składowych, ze wskaźnikiem rozmieszczenia poszczególnych gatunków α (fig. 2–7, tab. III):

$$\alpha = \frac{N_s}{N_r},$$

gdzie N_s określa liczebność gatunku na sosenkach, N_r – na wrzosie.

Stwierdzono istnienie trzech typów korelacji między powyższym wskaźnikiem, udziałem w zespole na wrzosie i udziałem w zespole na sosenkach. Pierwszy typ korelacji występujący u gatunku dominującego w tym środowisku – *Oxyopes ramosus* (Panz.) polega na tym, że zwiększeniu się liczby osobników gatunku w zespole na wrzosie towarzyszy zwiększenie się liczby osobników tego gatunku w zespole na sosenkach. Dominacja jego rośnie w zespołach obu warstw. Jest to gatunek zwyciężający w konkurencji inne gatunki (fig. 3) Drugi typ korelacji, występujący u gatunku niezbyt liczebnego i rzadkiego w Polsce *Philaeus chrysops* (Poda), polega na procesie odwrotnym: zmniejszaniu się liczby osobników w zespole jednej warstwy towarzyszy zmniejszanie się jej w drugiej warstwie (fig. 5). Taki gatunek należy do gatunków „słabych" w zespole, nie wytrzymujących konkurencji z innymi gatunkami. Stopień jego dominacji w zespole maleje. Trzeci typ korelacji występuje u gatunków zdolnych do kompensacji w wyborze warstwy, w której żyją np. *Xysticus cristatus* (Clerck) i *Clubiona trivialis* C.L. Koch. Zwiększeniu się ich udziału w zespole pająków jednej warstwy towarzyszy ubytek w drugiej (fig. 6, 7). Konkurencja ma na nie wpływ, ale potrafią one przy większym nacisku konkurencyjnym na wrzosie zwiększyć udział swych populacji w drugiej warstwie.

AUTHOR'S ADDRESS:
Dr. Jadwiga Łuczak
Institute of Ecology,
Warszawa, ul. Nowy Świat 72,
Poland.