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DIFFERENCES IN THE STRUCTURE OF COMMUNITIES  
OF WEB SPIDERS IN ONE TYPE  
OF ENVIRONMENT (YOUNG PINE FOREST)\*

The comparison carried out of 8 communities of web spiders in the field and shrub layers of a young pine forest. The spider communities were investigated on stands differing as to the age of the pine trees. It was found that one type of association occurs on all the stands. The characters of community structure such as specific composition, total abundance, abundance of common species and frequency are correlated with the age of the pine trees. More species and individuals occur in the older plantations. The hypothesis was put forward that in a year with weather "favourable" to the xerophilous species examined, interspecies relations exert an important influence on the formation of abundance relations in the community, while in an "unfavourable" year as regards weather, it is the prevailing climatic conditions which do so.

The aim of the present study is to describe and compare the structure of communities of web spiders occurring in different stands in one type of environment. The problem consists of whether the same type of community (association) is formed in uniform (or similar) habitats, and what the differences and similarities are between definite communities living in different patches of the habitat, and finally which factors are responsible for these differences. The question arises to what degree the structural elements of the community, usually distinguished and examined by ecologists (qualitative and quantitative composition of the community and the distribution in space of the individuals of different

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species in the community) are variable, and what ecological factors affect this variability.

Investigation of the variability of characters of the structure can be made on different collective units. Biocenological literature as a whole is an example of this. Taking different criteria for distinguishing biocenotic units as a basis, different types of communities have been described – life forms, synusia, associations, biocenoses etc. Describing the criteria of biocenotic units is not, however, the aim of this paper; what is in fact essential is to distinguish the natural elementary biocenotic unit in a group of spiders, as only in this case is an analysis of the variability of structural characters endowed with a deeper ecological sense and may contribute to a solution of the problem of the relation of intrabiocenotic units to the habitat. This unit may be formed by spiders belonging to one life form (Remane 1943, Kühnelt 1943, 1951, Tischler 1955, Balogh 1958), since each life form plays some definite role in the biocenosis which only it can fulfil. On this account it has characteristic properties of the biocenotic units.

The concept of the life form, which arose during Humboldt's time, and was worked out in greater detail for botanical purposes by Warming (1909), Gams (1918) and Raunkiaer (1934), next shifted in a zoo-ecological direction and was defined by Remane (1943) as follows: to one life form belong "organisms which in connection with a similar way of life create a complex of similar structures, in such a way that it is possible to draw conclusions as to their way of life from the structure itself". Remane is against the use of the concept of the life form only in relation to organisms having a common living space or solely on the basis of a similarity in the habitus of the animals, and introduces to this concept similarity of adaptations, which may occur in species which have no origin in common.

In the present study web spiders have been chosen from among the whole of spider fauna because of their abundance in these layers (Bilsing 1920) and their important role as predators (Bristowe 1939–1941) in the economics of the forest biocenose (Vité 1953). The web spiders examined are characterised by similarity of life form, that is: similarity of distribution (they live in one habitat and in one horizontal layer), similarity of way of life, adaptations and the way in which they obtain food, similarity in the kind of food consumed. The above common features decidedly distinguish the species examined from among other species co-occurrent with them in nature, providing grounds for treating the communities of species encountered together in defined habitats as ecological units, since they carry out functions in the biocenosis which distinguish them from other communities of spiders and other animals. Kühnelt (1952) who is in favour of investigation both of whole biocenoses and parts of them, writes: "It is particularly important to establish the specialisation of different members of the biocenosis. It is not a question here simply of producers or consumers of various types ..... but most often of characteristic specialised species, which



exhibit very definite requirements both as to habitat conditions and to their way of feeding”.

Petrusewicz (1938) divided spiders into the following ecological groups: web spiders, wandering and jumping spiders (*Lycosidae*, *Salticidae*) and ambushing spiders (*Thomisidae*).

Balogh (Balogh and Loksa 1948) divides spiders into three life forms, distributed into two communities according to layer (Schichtgemeinschaften): “ground level community” (Die Schichtgemeinschaft der Bodenschicht) and “plant-living community” (Schichtgemeinschaft der Feldschicht), each of which includes three life forms termed by the author “syntrophia” (Balogh 1946): 1) spiders spinning webs to catch their victims, 2) spiders catching their victims by chasing them, 3) spiders jumping on to their victims.

I have accepted the above criteria for classifying spiders given by Petrusewicz and Balogh, and have analysed the life form of web spiders distributed in the field layer vegetation and in young pine trees (the shrub layer) of pine tree plantations, treating this life form as a natural biocenotic unit (according to Balogh “syntrophium”); in order to avoid introducing new terms I have called them “ommunities” in the present paper. Petrusewicz (1936) gives a very loose definition of the term “community”, which may be taken as applying to different material: “the term community would therefore cover all groups of living beings, and therefore such terms as bio-, zoo- and phytocenosis, synusia, faunula, etc. There is only one limitation: that there should be a connection, even if loose and indirect through the substratum, but at least regular, between the components of the community”. In the case of the present paper a definite ecological unit is implicit in the general term “community”.

When differentiating between animal communities of different habitats (Petrusewicz 1937) zoocenologists often chose the method based on an analysis of characters of the animal community (Petrusewicz 1938, Kontkanen 1950a, 1950b, 1957, Haarlov 1960 and many others), since it is a well known fact that distribution of animal species does not correspond strictly to the distribution of plant associations: animal communities often coincide with fairly large phytocenological units, considerably larger than associations (Thiele 1956) or, particularly in the case of small animals, are distributed in patches in the biotope constituting a complete phytocenological whole.

Petrusewicz (1938) formulates this question as follows: “animal communities or associations may be distinguished from two points of view – 1) on the principle of uniformity of the habitat and 2) on the principle of uniformity of the fauna. The first method is applied in investigating the animals of a given habitat, in practice most often a given plant association. After examination of a large number of stands of one type of environment, the animals as a whole living there are generalised as a type of community or an association. This is the method of indirect distinguishing of associations. The second method is the direct one”. The present study is concerned with investigating whether one



association occurs on different stands in one type of habitat, and which characters of this association are constant and which variable, depending on the differing intensity of the factors acting in the given section of the habitat.

Examination of animal communities according to defined plant associations has been made for a considerable time, and there is a large amount of literature on this subject, e.g. Książkówna (1936), Renkonen (1938), Lowrie (1948), Mikulska (1950), Quézel and Verdier (1953) and Thiele (1956).

In the present study several stands were selected in one type of habitat and the distributions occurring on these areas compared with the aim of determining the degree of similarity between communities of spiders, irrespective of whether similar communities occur elsewhere in completely different conditions of the habitat.

It may of course be anticipated that the communities examined will be very similar to each other. In similar habitats the specific composition should be the same: this was checked by Tretzel (1955), who formed a theoretical community which proved to be similar to a high degree to that examined empirically. The question of dominating species, on the other hand, is not so simple and easy to foresee and a check should be made to see whether it is always the same species which dominates, or whether variation in domination takes place. It would seem, however, to be especially interesting to determine the levels of abundance of the communities of spiders examined and of each more important species, together with their structure of domination and constancy, which up to the present have been investigated in very few studies only. Barnes (Barnes, H. and Barnes, B. 1955) confirmed the existence of an abstract community (or association) of spiders in open spaces covered chiefly by grass of the genus *Andropogon*, and also analysed domination, frequency, presence and constancy.

In comparing the structure of defined communities of spiders in one synusia and one syntrophium on different stands in one type of environment, according to different phytocenological indices (Poore 1956), differences in this structure can be observed; these differences can be correlated with the factors distinguished as more important, which vary in the given type of habitat. If the characters distinguished of the structure of the community prove to be correlated with a variable factor – there is considerable probability that they are dependent on it. Certain hypotheses can be formed in this way as to the dependence of the community on different factors of the habitat.

#### METHODS

A total of eight stands were chosen in a young pine plantation, growing among heather, in the neighbourhood of Dziekanów Leśny, on the edge of the Kampinos Forest, distributed over a space of several km., which – as belonging to one stage of succession (pine wood) – formed a development sequence within this stage (Allee et al. 1950); they differed from each other as to the age of



the small pine trees, the presence of other plants (birches, small oak trees or juniper bushes), degree of compactness of the forest stand, neighbourhood of other biocenoses (dunes, older pine wood), different degree of insolation and of humidity. In August and September, 1959 and 1960, five series of quantitative samples were taken both years on each stand from heather and from young pine trees, with the purpose of investigating the characters of the community structure. Quantitative samples were taken from the heather with an entomological sweep net; one series consisted of 10 samples, each of 25 strokes of the net. A total of 50 samples (1250 strokes) were taken from each stand in each of the study years, giving a total of 800 samples (20,000 strokes) in both the study years. Samples from the small pine trees were taken by shaking the branches over an open umbrella. One series consisted of the results of shaking 40 small pine trees (in the case of smaller trees the whole tree was shaken – with larger ones from 3–4 branches per tree). A total of 5 series was taken (shakings from 200 small pine trees) on each stand in the given year, giving a total of 80 series (shakings from 3200 small pine trees) in both the study years. For statistical purposes some series were divided when shaking into 8 samples: a sample consisted of spider material collected by shaking 5 small pine trees. The time observation method was applied to the investigation of the population of large argiopids.

A total of 39 species of web spiders, 7790 specimens, were captured on all the stands, consisting of small web spiders (up to 5 mm.) – 7110 specimens; medium web spiders (up to 10 mm.) – 410; large web spiders were not collected but counted by the time observation method (1/2 hour on each area); 270 individuals were observed.

In previous papers (Łuczak 1953, 1954, 1959 and also Karpiński 1956) it was found that August and September form the period of the greatest abundance and maximum equilibrium in the association of forest spiders distributed in the field and shrub layers, i.e. abundance and domination relations and the specific composition remain relatively constant. The young forms of the overwhelming majority of species characteristic of these layers then appear in both layers, forming a uniform and very slightly variable community of species. On this account – analysing the early autumn aspect of a spider association in the higher layers of vegetation – it is easiest to investigate the characters of its structure.

Assessment of the suitability of the material obtained by sweep net for investigation of the abundance and variations in numbers was made in papers by Łuczak (1958), Łuczak and Wierzbowska (1959). Confirmation was given in these works of the opinion held by Carpenter (1936), Kontkanen (1950a) and Barnes, H., Barnes, B. (1955) as to the convenience and advantages of the sweep net method for purposes of statistical treatment of variations in numbers and other characters of the community structure of certain communities of insects and spiders in habitats with homogeneous vegetation; it was also found that the length of the series of samples taken once only on each stand examined can and should be about 10. Spider material from this number of samples



ensures a sufficiently accurate estimate of their abundance in the area, reflects the fluctuations in numbers of some of the species richer in individuals and gives the true proportions of numbers for each of the species in the community.

All the spiders which fell into the sweep-net and into the entomological umbrella were collected, but only the group of web spiders in this material which were more numerous than other groups of spiders in these layers (Bilasing 1920) were used for the purposes of this study. The community of web spiders in the field layer and on the small pine trees on each stand were considered separately (a total of 16 communities were therefore analysed).

Comparison of the spider communities was made by analysing several important characters of the community: the specific composition, abundance, domination and frequency. Analysis was made by direct comparison with the criterion of statistical reality of differences and by the method of indices used in phytocenological examinations. Calculation was made of the Sørensen ( $QS$ ) index of specific similarity (Sørensen 1948), index of similarity of domination [the so-called Renkonen number ( $Re$ )] (Renkonen 1938, 1949), index of similarity of constancy of species (the so-called Kulczyński number ( $Ku$ ) Kulczyński 1928). All these indices are affected by the size of the sample and vary according to it. I used a collective sample, which contained material obtained from 50 smaller samples, each composed of 25 strokes of the net over the heather. From an analysis of the curve "species-size of sample" (p. 17) it will be seen that the number and size of the samples are sufficient to investigate the specific composition, abundance, domination and frequency relations of constant species.

The indices give only a general orientation as to the similarity of the communities defined on the basis of the numerical value of the index, which is established by comparing the communities in turn (each community with each of the others). On the basis of the numerical values obtained, some plant sociologists and zoocenologists (such Polish plant sociologists as Matuszkiewicz, A. 1958, Matuszkiewicz W., Traczyk, H., Traczyk, T. 1958, and zoologists Renkonen 1938, Kontkanen 1950a, Macfadyen 1954, Haarlov 1960) drew up diagrams in the form of a "trellis diagram", in order to obtain a graphic picture illustrating the similarities and differences between communities. This method was introduced to plant sociology by Kulczyński (1940), modelling it on studies by Czekanowski. In the present study I have also arranged the indices obtained in diagrams, since this method makes it easy to distinguish variants of the association more or less similar to each other as regards a given character. Index  $QS$  defines the qualitative feature of the spider community examined, indices  $Re$  and  $Ku$ , its quantitative features.

Kontkanen (1950a, 1950b, 1957) and others used Kulczyński's method for distinguishing animal communities from the abundant material collected from different habitats; they, like Lityński (1938), based their findings on the assumption that structural characters such as the qualitative composition of the community, constancy of species or domination — are similar in similar com-



munities (with a sufficiently large scope of variation of the indices). In this study these characters serve to analyse and describe one association, and to investigate its variations depending on factors differentiating the study areas. The scope of the differences occurring here is considerably smaller than in Kontkanen's material, but with a suitable selection of more subtly differentiated scopes of variation of indices, an increase in sensitiveness of the method was obtained in order to reveal different pictures of one association distributed in differentiated stands in one type of environment as similar communities. The scopes of variation of the indices of similarity were so chosen as to ensure maximum sharpness of the picture of differentiation when arranged in a trellis diagram. In this way the method, depending on the way in which the scope of indices is arranged, may also serve to distinguish different associations from the faunistic or floristic material (in the case of Kulczyński and Kontkanen) and to discover different variants of structure within one association (in the case of the present study).

Making use of Kulczyński's method for other purposes, I also altered the way in which the indices of similarity were arranged in the trellis diagram, not in a search for the best way of arranging them (the values of the indices put in order one after another in order of similarity), but according to succession of stands established beforehand: from the oldest plantation down to the youngest. I wanted to discover whether differentiation exists between the structural characters of the communities in relation to the age sequence of young pine tree plantations and to what extent correlation takes place.

I used the following systematic books for identification of spiders: Chyzer, C. and Kulczyński, W. — *Araneae Hungariae* I (1891), II (1894); Locket, G. H. and Millidge, A. F. — *British spiders* I (1951), II (1953), Roewer, C. Fr. — 4 Ordnung: *Araneae* — *Echte oder Webspinnen* — *Die Tierwelt Mitteleuropas*, V. III Spinnentiere; Simon, E. — *Les Arachnides de France*, VI. *Synopsis general et catalogue des espèces francaises de l'ordre des Araneae* (1914, 1926, 1929, 1933, 1937), 2–5 parts published L. Berland et L. Fage; Wiehle, H. v. 23 Spinnentiere oder *Arachnoidea, Araneidae*, *Tierwelt Deutschlands* (1931); Wiehle, H. v. 33 Spinnentiere oder *Arachnoidea*, VIII. *Theridiidae* *Tierwelt Deutschlands* (1937); Wiehle, H. v. 42. Spinnentiere oder *Arachnoidea — Mimetidae*, *Tierwelt Deutschlands*; Wiehle, H. v. 44. Spinnentiere oder *Arachnoidea*, 28 Familie *Linyphidae* — *Baldachspinnen. Tierwelt Deutschlands* (1956).

#### DESCRIPTION OF THE STUDY AREAS

##### Stand A

This is a young pine wood with considerable admixture of birches, growing on a stretch of dunes. Pine trees cover about 50% of the area (not evenly), and birch trees about 20%, total about 60%. The pines are of different ages and



heights: from 1.5 to 6.0 m., most often from 2.5 to 4.0 m. The age of the pines varies from 11 to 16 years; even the smallest trees, about 1.5 m. in height, have from 10 to 15 rings of branches. Birch trees occur in all layers, from ground vegetation to the highest layer at 6–8 m., above the tops of the pine trees. In the field and shrub layers there is an admixture of oak, aspen, juniper and *Frangula alnus*. Heather occurs in patches, covering in general about 40% of the area and in places devoid of trees or where the trees are smaller – up to 70%. In places heather occurs in larger stretches or even small islands. A few small patches of bare sand can also be seen – the white layer of humus is very thin, about 5 cm., and under it is a light-coloured whitish sand with rust-coloured stains. Twenty-one species of vascular plants were found. Seven species of lichens (collected once only) were found in this area, but they all occur in very small quantities only. There are no compact, grey stains of lichens, such as there are on stands E, F, G, and the greater part of the area not covered with heather is occupied by fallen pine needles. On these grounds it was found that this wood grows on the *Pineto-Vaccinietum myrtilli* stand (presence in the herb vegetation of species characteristic of this group and absence of dune associations species of the order *Corynephorretalia*).

Of all the areas examined, this area is covered by the oldest forest, strongly shading the ground. The average growth of the pine trees and average number of rings of branches is greatest here.

#### Stand B

Young pine plantation on dunes, on flat ground. The pines, planted in rows which are still distinctly visible, cover on an average about 70% of the area, although this cover is not uniform: in places 50%, in places 80%, and even 90%; there are also bare places without trees. The path on which samples were taken is similar in appearance to the other treeless places. The height of the pines is from 1.5 to 5 m. (numerous trees 3 m. high) age of the pine trees from 10 to 13 years. There is an admixture in the upper layer of *Pinus Banksiana* and *Betula pubescens* (up to 6 m. in height); in the shrub layer: *Quercus robur*, *Juniperus communis*, *Populus tremula*, and *Sorbus aucuparia*.

The herb vegetation is composed of heather covering about 70% of the area, particularly in treeless places. There are a few higher plants among the heather. Large patches of heather are separated by stretches of almost bare earth, on which only moss and lichens grow, and a very few vascular plants. Here and there are light spots of almost completely bare sand.

Inspection made twice of the area revealed 23 species of vascular plants, 7 species of lichens and small patches of moss. The specific composition of the vegetation suggests that this young pine plantation is growing on a *Pineto-Vaccinietum myrtilli* stand. Characteristic species occur in the field and shrub layers, and in places not shaded by trees lichens grow more abundantly, with



a few scattered vascular plants characteristic of a *Pineto-Vaccinietum myrtilli cladonietosum* forest (Tab. I).

This young pine plantation is among the oldest of those examined and is inferior in this respect only to the plantation on stand A. The densely covered parts of this stand belong to the most densely afforested, but the path and large treeless patches of this area render it more similar to the younger and drier areas.

#### Stand C

Young pine plantation on dunes, on flat ground. The pines cover about 50% of the area, forming distinct and fairly compact rows. This plantation is among the most densely afforested of all the areas examined. The height of the trees is from 1.0 to 3.5 m., most often from 1.7 to 3.0 m., and therefore relatively even. The age of the pine trees varies (6–12 years, most often 9).

There is a certain admixture of birch: these are small trees growing among the herb vegetation, a large number of trees of medium height similar to the height of the majority of pine trees, and tall trees from 5 to 8 m. On the periphery of the stand, by the roadsides, there are many tall birch trees. The few specimens of juniper bushes are from 1 to 2 m. in height, and there are very small oak trees and aspens in the field layer.

The field layer is composed of heather covering about 60–70% of the area. On the few treeless patches heather covers up to 90% of the area. There is no bare sand visible at all. A total of 16 species of higher plants was found, but they occur in very small numbers of specimens and are very difficult to find among the heather. Lichens do not occupy a large area, but occur in a relatively large number (7).

In general this stand is similar to stand D, but the trees are older, bigger and shade the ground to a far greater degree.

From the phytosociological aspect this pine plantation occupies an intermediate station between group A B D, growing on a *Pineto-Vaccinietum myrtilli* stand, and group G F E growing on a *Pineto-vaccinietum myrtilli cladonietosum* forest.

#### Stand D

Young pine plantation on dunes. *Pinus silvestris* covers more or less uniformly 30–40% of the area, forming distinctly uniform rows, although here and there are treeless patches. The trees are younger than on stands A, B and C, in general from 7 to 11 years old (most often 8); height of the trees from 1.0 to 2.5 m., – and is therefore in comparison with other areas very little differentiated. There is a fairly considerable admixture of birch about 4 m. in height, and



Species of plants occurring on the stands examined

Tab. I

Species occurring on all stands (7 or 8)	Stands								Groups	
	A	D	B	C	E	F	G	H		
<i>Pinus silvestris</i>	+	+	+	+	+	+	+	+	I	
<i>Betula verrucosa</i>	+	+	+	+	+	+		+		
<i>Juniperus communis</i>	+	+	+	+	+	+	+	+		
<i>Calluna vulgaris</i>	+	+	+	+	+	+	+	+		
<i>Pteridium aquilinum</i>	+	+	+	+	+	+	+	+		
<i>Festuca ovina</i>	+	+	+	+	+	+	+	+		
<i>Rumex acetosella</i>	+	+	+	+		+	+	+		
<i>Quercus pedunculata</i>	+		+	+	+	+		+		
<i>Populus tremula</i>	+	+	+	+	+		+	+		
<i>Cladonia silvatica</i>	+	+	+	+	+	+	+			
<i>Cladonia furcata</i>	+	+	+	+	+	+	+			
<i>Cladonia cornutoradiata</i>	+	+	+	+		+	+			
Differential species of <i>Pineto-Vaccinietum</i> <i>myrtilli</i> stands										
<i>Molinia coerulea</i>	+	+	+							II
<i>Convallaria maialis</i>	+	+	+							
<i>Rubus</i> sp	+	+	+			+				
<i>Vaccinium myrtillos</i>	+	+		+						
<i>Luzula pilosa</i>	+	+	+		+		+			
<i>Frangula alnus</i>	+	+						+		
<i>Vaccinium vitis idea</i>	+		+	+				+		
<i>Chamenerion angustifolius</i>		+	+							
<i>Cladonia cornuta</i>	+	+	+							
<i>Cladonia deformis</i>	+		+							
<i>Cladonia fimbriata</i>		+	+							
Differential species of <i>Pineto-Vaccinietum</i> <i>myrtilli cladonietosum</i> stands										
<i>Carex ericetorum</i>			+	+	+	+	+	+	III	
<i>Hieracium pilosella</i>			+	+	+	+	+	+		
<i>Solidago Virga-aurea</i>			+	+		+	+	+		







in the shrub layer — a few specimens of juniper, aspen and *Frangula alnus*.

Heather covers almost uniformly 90% of the area, reaching even quite deeply under the branches of the trees. There are a very few small bare patches without heather. On May 9th 1960 the heather had grown very little after the winter, but by August regrowth had improved considerably. Only 15 species of vascular plants were found, but these included species typical of *Pineto-Vaccinietum myrtilli*. There were small patches of moss, chiefly *Entodon Schreberi*. Lichens were even scantier (4 species covering very little area), with complete absence of *Cladonia sylvatica*, *Cl. rangiferina* and *Cetraria islandica*.

This stand is highly uniform as regards the height of the trees and heather cover, and belongs among the younger plantations.

### Stand E

Young pine plantation on dunes. The plantation is separated from the considerably older pine wood by a road. The pines cover about 40% of the area, but not uniformly. There are treeless patches. The growth and number of the rings of branches of the pines differ greatly. The majority of the pines are from 2 to 3 m. in height, but height varies from 0.5 to 4.0 m., and the age of the majority of the pines is from 8 to 10 years, varying from 5 to 14. There are two groups of pines. In addition to the older trees, scattered clumps of younger pines were planted which are now about 5 years old, and vary from 0.5 to 1.0 m. in height. There is an admixture of fairly high birches, oaks, pines (*Pinus Banksiana*) and aspens, lower junipers and *Populus alba*. There are more large deciduous trees by the roadside.

The heather grows in patches over the area, occupying a total of about 40% of the whole area. There are patches of heather occupying 70% of the area, and spots without heather. By the roadside, nearer the edge of the study area, there is more heather. Small birch trees (up to 20 cm. in height) grow among the heather. Large patches of lichens and small mosses cover the places without heather; *Cladonia sylvatica*, *Cl. rangiferina* and *Cetraria islandica* predominate. A total of 8 species of lichens were counted. Fourteen species of higher plants were counted here; there are very few in the field layer and they occur in small numbers; dune-growing species such as *Spergula vernalis* are encountered among them. This young pine plantation grows on a *Pineto-Vaccinietum myrtilli cladonietosum* stand.

Symptoms of drought could be seen distinctly on this stand in May (dying, rust-coloured small pine trees and junipers, dried-up heather). In August 1960 considerable improvement in the condition of the heather was noted (strong reaction to rain). Distinct traces of ground frosts were noticeable in May 1960 (frostbitten leaves of oak trees at the height of an average man).



## Stand F

Young pine forest on dunes, situated close to stand E. The area is tilted slightly towards the west, in the direction of the forest road, on the other side of which there is a high pine wood.

The pines cover, unevenly, about 50% of the area, but there are patches without trees. The growth of the trees varies considerably, and it is difficult to say which height is predominant. There are specimens from 0.3 to 3.5 m. in height and higher. The age of the younger pines is from 4 to 5 years, the older from 7 to 10 years. The places on which the younger trees have been planted in clumps can be distinctly seen, as in the case of area E. There is an admixture of high birch trees (up to 10 m.). There are more higher trees on the periphery of this study area.

Heather occurs in patches, covering 40% of the area. In the places not covered by heather there are large patches of lichens and even bare sand. Seventeen species of vascular plants were counted: the specimens of vascular plants occurring in the field layer are few in number. Among them dune-living specimens are encountered, such as *Spergula vernalis*, *Scleranthus*, *Corynephorus canescens*. This young pine plantation also grows on a *Pineto-Vaccinietum myrtilli cladonietosum* forest.

The symptoms of drought visible in May 1960 had disappeared in August 1960 and the condition of the heather had greatly improved. The carpet of heather had become considerably richer by August.

This plantation is markedly similar to plantation E, differing only as to the smaller admixture of deciduous trees, far higher and older than in area E.

## Stand G

A young pine plantation growing on sand. In the immediate neighbourhood there are dunes which have only recently been afforested, with large extents of bare sand, surrounding the study area on several sides. Some dunes are situated on a higher level than the area examined, others lower.

The pines cover 30% of the area here, but not evenly. They are in general about 7 to 10 years old (the majority 8 to 9) and differ greatly in height: from 0.7 to 2.7 m.; there is a large number of trees varying in height from 1 to 2.5 m., but even these smallest trees have not less than 6 rings of branches. There is an admixture of a few specimens of *Pinus Banksiana* and juniper.

There is a large amount of heather; large uniform patches cover about 70% of the area, and within the patches themselves, up to 90% of the surface. The heather had only very feebly regrown after the winter in May 1960. In bare places, without trees or heather, there was light-coloured sand and small mosses with a large amount of lichens forming a grey carpet. Sixteen species of vascular



plants were counted here, but the number of individuals of each species is small. There are typical dune and sand species here, such as *Corynephorus canescens*, *Spergula vernalis*. On these grounds this plantation may be classified with the *Pineto-Vaccinietum myrtilli cladonietosum* association.

There are signs of drought (particularly in May 1960) on the plants: dry leaves of *Pteridium aquilinum*, a large mass of dry branches of heather. The pine plantation in this area is among the youngest of those studied.

### Stand H ("hollow")

A basin-shaped hollow between dunes with a flat bottom. The dunes are situated on three sides of the hollow, in general afforested, and separate this area from the Łuze meadows. The soil is sandy and light in colour; the pH of the surface layer is 5. The place is covered unevenly by pine (*Pinus silvestris*) of varying heights: 0.3–3.5 m., the majority about 1–2 m. The greater part of the pines are from 7 to 10 years old, their height varying considerably. In places, however, there are very small pine trees 0.5 m. in height and about 4–5 years old. The pines cover about 40–50% of the area. In the tree layer specimens of birch also occur (*Betula pubescens*) 4–5 m. in height, far higher than the highest pines. The pines of 1–2 m. in height are most often equalled by the admixture occurring in small numbers of *Populus tremula*, *Juniperus communis* and lower birches. *Quercus robur* and *Frangula alnus* only occur in the field layer vegetation.

Heather grows in large patches covering 60–80% of the study area. Traces of the effects of drought can be seen, which (despite the fact that they were not most distinctly marked) were not completely effaced after the rain falling in July 1960 and at the beginning of August 1960.

There are spots without trees or heather in places, on which lichens, small mosses and higher plants grow in scattered clumps (grasses) or in loose patches, or even singly. The bare sand shows through.

Thirty-four species of vascular plants were found, although all the species occur in small numbers. The lichens were not collected from this area.

This young plantation, although here and there the rows of planted trees can be distinguished, gives the impression at the first glance of being naturally grown and it is this "natural" appearance which distinguishes it from the seven other study areas. A certain "naturalness" of this young plantation is also evident in the largest number of species of vascular plants in comparison with all the other stands (23 and 21 species on stands B and A and 14–17 on others).

Phytosociological analysis showed that this plantation has grown on a *Pineto-Quercetum* stand.

This habitat is markedly mosaic-like in character and the trees and bushes growing here only slightly shade the soil.



Using the above descriptions and a table of phytosociological surveys as a basis (Tab. I) we can describe the habitats examined as, generally speaking, young pine plantations with heather in the field-layer, growing on dry and sandy soils, but not completely identical. The specific composition both of vascular plants and of lichens, makes it possible to divide the plantations examined into three groups:

1. Stands *A*, *D* and *B* are young plantations growing on *Pineto-Vaccinietum myrtilli* habitat. They are characterised by the occurrence in the field- and shrub-layer of 8 differential species (Tab. I, group II), of which only a few can be found in the remaining stands once or twice. These plantations are also distinguished by the lack of species occurring in *Pineto-Vaccinietum myrtilli cladonietosum* habitats (group III) and on dunes (group V). Stand *B* is distinguished from the two remaining areas in this group by the presence of 3 species (group III), which are rather characteristic of drier habitats, and a larger amount of lichens, growing chiefly on the path and in large treeless patches.

2. Stands *F* and *G* are pine plantations growing on *Pineto-Vaccinietum myrtilli cladonietosum* stands. They are distinguished by the occurrence of a different group of differential species, typical of such habitats (group III) and the occurrence of dune and sandy species (group V).

3. Stands *C* and *E* we can classify as between *A D B* on the one side, and *F G* on the other, *C* being more similar to the first of these groups, and *E* distinctly to the second. This latter phenomenon is markedly evident in the ground vegetation, when collecting the lichens which formed there large, grey patches, as distinct from the darker heather. Seedlings of the dune species *Spergula vernalis* were also found there. The absence of certain species of vascular plants in the field layer in the summer of 1960 might be the result of the catastrophic drought which visited this region in the spring and at the beginning of the summer of 1960, and which affected this particular area most strongly.

4. The young plantation on stand *H* represents a separate community with a relatively large number of vascular plants. Nine species of this number do not occur on any other of the study areas. Although all the dune-living species found in the investigations occur on this stand (which can be explained by the immediate neighbourhood of the dunes, in places not even afforested), it must however be taken — on the grounds of the presence of the 8 species referred to (group IV) that this plantation is growing on a *Pineto-Quercetum* stand.

None of these floristic differences are, however very distinct, as they apply almost exclusively to the forest field layer and, to a very slight degree only, to the shrub layer, and are not evident in the tree layer (even where this is very low); these are all artificially planted tree plantations constituting successive stages, which only at some time in the future will be transformed, probably into typical associations belonging to the *Pineto-Vaccinietum myrtilli*, *Pineto-Vaccinietum myrtilli cladonietosum*, *Pineto-Quercetum* associations.

From the table given the great floristic similarities between all the study



stands can clearly be seen: 9 species (the majority of which are trees and bushes) occur in all the 8 young pine plantations or almost in all (6, 7) (Tab. I, group I). This similarity is however most marked in the same dominating species: *Pinus silvestris* in the upper layer and *Calluna vulgaris* in the field layer. Against the background of the general similarity (one type of environment) the phytosociological differences of the habitats described above are marked in the field layer, and also differences of another type of which the following were analysed: the age of the small pine trees, their height, the extent to which the pines cover the area, uniformity of the heather carpet, degree of humidity.

Two age groups can be distinguished – an older and a younger – in the plantations examined. Stands *A, B, C*, the small pines in which are in general from 9 to 16 years old, belong to the older group. They are of fairly uniform growth on each area. Using the most numerous pines as a basis, the gradient of age can be determined: the oldest plantation, in fact a young pine wood, about 16 years old, is stand *A*; the next, about 13 years old, is stand *B*, and about 12 years old, stand *C*. The remaining stands belong to the group of young tree plantations, about 7–9 years old, and it is difficult to determine a distinct age gradient here, especially that (apart from station *D*, most probably the oldest in this group and *G* – one of the youngest) the young pine trees occurring here vary greatly in growth. Stand *H* differs from stands *E* and *F* in that the patch-like additional planting of pines, so apparent on the other areas, is not so clearly visible; this feature and the difficulty in perceiving an arrangement in rows of pine trees and a relatively large number of species of vascular plants gives this area the apparent character of a natural forest stand.

The order according to age of the young tree plantations, taking into consideration the features described above, may be arranged as follows: *A, B, C – D – E, F – H, G* (or *G, H*). The height of the pines in the group of older plantations is in accordance with their age (*A, B, C*), but in the group of younger plantations growth is more varied, and it is difficult to place them in order of height.

The extent to which the area is covered by the pine trees is greatest on stand *B* (80% in the wooded parts; this stand has several large patches on which heather only grows) then in the following order on stands *A, C, H, F* (about 50%), the smallest being on stands *E, D, G* (30%–40%).

The densest carpet of heather occurs on stands *D, C, G* (70–90%), then in order on stands *B* and *H* (about 70%); the least compact and uniform carpet of heather grows on stands *A, E* and *F* (about 40–50%). There is distinctly less heather on these three last stands and it is more patchily distributed.

The largest number of species of higher plants occurs on stand *H* (“hollow” – 34), then on *B* (23) and *A* (21), and then on *F, C, D, G, E* (from 14 to 16 species).

As an index of the differences in humidity on the stands examined I have accepted the relative humidity measured on 7 stands on October 6th 1960 (Tab. II). This is the average of three measurements made by hygrometer at a height



## Collective characteristics of the study areas

Tab. II

Features of habitat		Stands examined in order of age							
		A	B	C	D	E	F	G	H
Covered by pines (percentage)	80		x						
	50 30 - 40	x		x	x	x	x	x	x
Covered by heather (percentage)	70 - 90			x	x			x	
	70 70 - 40	x	x			x	x		x
Number of species of higher plants	34								x
	23 - 21 14 - 16	x	x	x	x	x	x	x	
Relative atmospheric humidity		64.67	65.33	55.67	58.67	54.67	59.67	51.67	-

of 1 m. above the ground. The rapidity of the increase of the relative humidity of the air in the study area depends on the degree of total humidity in the given place, which also may serve as an index of differences in moisture content. The height of the indices gives a general indication of the high degree of dryness of the stands examined, and the differences in their values follow a pattern roughly in accordance with the age of the young pine trees: the highest values are exhibited by the index of humidity in the two oldest plantations.

#### RATIO OF NUMBER OF SPECIES CAPTURED TO THE SIZE OF SERIES

One of the first problems which confront the research worker investigating animal communities (and plant associations) is the question as to whether all the more important species for the given environment have been captured by the quantitative capture method used.

It is a generally known thing that the number of species, with an increase in the size of the sampling area or in the capture series, at first rises sharply, then the increase in the number of species in samples declines. Plant sociologists investigated this phenomenon by means of "species-area" diagrams, marking on the abscissa - the size of the sampling area, and on the ordinate the number of species occurring in these areas. On the diagram the curve of number of species usually rises rapidly at first and then tends to flatten out into an almost straight line. The section of curve at the place where the curve running sharply upwards breaks off, and becomes increasing horizontal, indicates the minimal species area, which should be investigated in order to observe all the more important species of the environment studied. This is, as Braun-



Blanquet (1932) puts it "the smallest area capable of containing an adequate representation of the association". The impossibility of empirical determination of the final section of the curve and the difficulty of establishing the point of inflection of the curve led to criticism of the "minimal species area" theory (Hopkins 1955, 1957, Greig-Smith 1957). Despite the theoretical difficulties in interpretation of the "species-area" curve, ecologists acknowledge its importance as a useful practical tool in ecological research on plant associations (Poore 1955a, 1955b), since by this means it is possible approximately to estimate whether the size of the sampling area has been properly established.

The first of the zoologists to use the classic "species-area" method was Haarlov (1960) in ecological investigations on the arthropods of Danish soils, but Beklemišev, as early as 1931, investigated the extent of influx of species with the increase in area, making use of the modified Arrhenius formula (Tarwid 1956).

The increase in area on which the increase in number of species is investigated may be measured by the number of samples taken from the stands examined; in homogeneous environments, such as, e.g. in heather, each sample contains spiders taken from relatively uniform areas. This is a modification of the classic method which is essential when making captures by sweep-net.

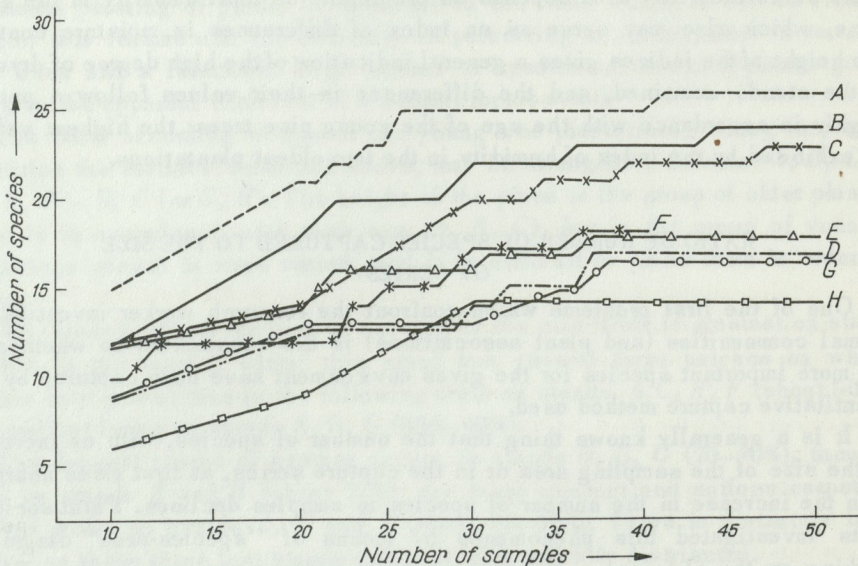


Fig. 1. Curves of increase in the number of species of spiders in the field layer (web and wandering) together with increase in the number of samples (data from 1959)  
Stands A - H

Diagram (Fig. 1) illustrates how the number of species captured on each stand grows with the increase in the size of the sample (in the case under



discussion together with an increase in the number of uniform samples). All species of spiders caught by sweep-net on the stands examined were taken into consideration in the diagram — both web and wandering spiders. The method used consisted in totalling up the samples. The number of species in the second sample not occurring in the first is added to the number of species occurring in the first; the number of species in the third sample not occurring in the first and second sample is added to the total number of species in the first and second samples, etc. up to the sum of 50 samples<sup>1</sup>.

On stand *H* with even thirty samples the number of species is exhausted, which is indicated by the long horizontal section on the diagram of the curve. Not a single new species occurs among the following 20 samples. On stands *B* and *D* it is not until sample 37 that a relative exhaustion of the number of species takes place, and on area *G* — with the 38th sample. Other situations are shown by the curves of the further stands examined. On stand *C* it is true that the curve of number of species can be seen to rise far more gently after the 30th sample, but it does not resolve into a horizontal line and is “step-shaped”, which means that up to the 50th sample new, rarely distributed or fortuitous species continue to occur additionally. This may indicate the greater wealth of this stand compared with others, or, which is more probable, the greater degree of mosaic character of the habitat, which causes uneven distribution of species. The situation is similar on stand *F* — new species are constantly added, affecting the course followed by the curve. The curve on stand *A*, starting from the 41st, and on stand *E* from the 47th, sample, becomes horizontal and it may be anticipated that if these habitats were further investigated yet additional, different new species may occur with about one individual per several samples.

The following conclusions may be drawn from the above data. Stands *B*, *D*, *G* and *H* are poorer in species, or more homogeneous than the remainder and were fully exploited, even with regard to sparsely distributed species. Stand *A* is richer in species than the remainder, but 50 samples are amply sufficient for a relatively accurate knowledge of the specific composition of its spiders to be obtained; stands *C* and *E* however, are either richer in species than *A*, or the species are distributed in spots over them and therefore new species constantly occur in successive samples; 50 samples is too little to exhaust all the rare species occurring there. With regard to more numerous species, the method used shows that the number of samples taken is amply sufficient, since species represented in large numbers of individuals, common to all the areas, occur by

<sup>1</sup>As the spider material from the first two series of 10 samples each, was not divided up into separate samples, the joint number of species in the first series is calculated and included in the diagram in the form of one point. The second point of the curve indicates the joint number of species of the second series of captures not occurring in the first series. The next three series, the material of which was divided when making captures into each sample (10 samples in a series), give the number of species occurring additionally in each sample (30 points on the diagram).



the 15th sample at the latest (and in general considerably earlier), and common species represented by small numbers, by the 24th sample. The predominant species, *Mangora acalypha* (Walck.), occurred on all the areas in the first sample.

The method described above of drawing "species-area" curves has been criticised by some scientific workers (Goodall 1952, Greig-Smith 1957); the objection is made that rare and accessory species are given undue importance as the result of adding the samples together, by which the number of these species is, as it were, artificially increased in relation to the area. When totalling is used, the samples are not independent of each other: species occurring, for example, in samples no. 1, 2 or 3, covering a very small area, must occur in all the following samples, e.g. in the thirtieth sample which covers a large area. The above-mentioned authors recommend that when the size of the sample is increased (in this case when increasing the number of samples) use should be made of random samples taken separately, instead of increasing the samples by adding them together. This affects the modification of the course taken by the curves. With random samples, completely independent of each other, fewer species occur additionally, and therefore the curve is gentler, rises far more slowly and undoubtedly gives a truer picture of the distribution relations of the species in the area (particularly in regard to the rarer and less numerous species). Species distinguished by great and medium numbers of individuals are, however, caught in the first 15 samples. In the present study I have not dealt in detail with the ratio of number of species to the study area, and therefore the method of adding different samples together is completely sufficient to show that the size and number of samples accepted in this work is adequate for a relative qualitative exhaustion of the environment and the capture of all abundant species.

The level of number of species indicates that communities of spiders of all the stands can be divided into two groups. One group includes the communities on areas *A*, *B*, *C* (the oldest plantations), which are characterised by a larger number of species (44, 44, 45), the second – the communities of stands *D*, *E*, *F*, *G*, *H* (younger pine trees) which have a smaller number of species (36, 37, 37, 38, 39). Thus the analysis of curves of the number of species gives the first information as to differentiation between the study areas according to wealth of species, and possible the way in which they are distributed over the areas.

Figure 2 illustrates the increase in the number of species of small web spiders together with an increase in the number of samples. If we take the number of species caught on each stand in 50 samples as 100%, then in the first 10 samples we catch about 50% of the number of species (43–67%), in 20 samples about 70% (61–81%) and in the 30 from 80–90% (70–100%). As from the 38th sample no new species is found on the younger stands *D*, *E*, *F*, *G*, *H*, while the same applies to the older stands as follows – stand *A* – from the 41st sample, stand *B*, from the 44th sample, and stand *C*, from the 47th sample.



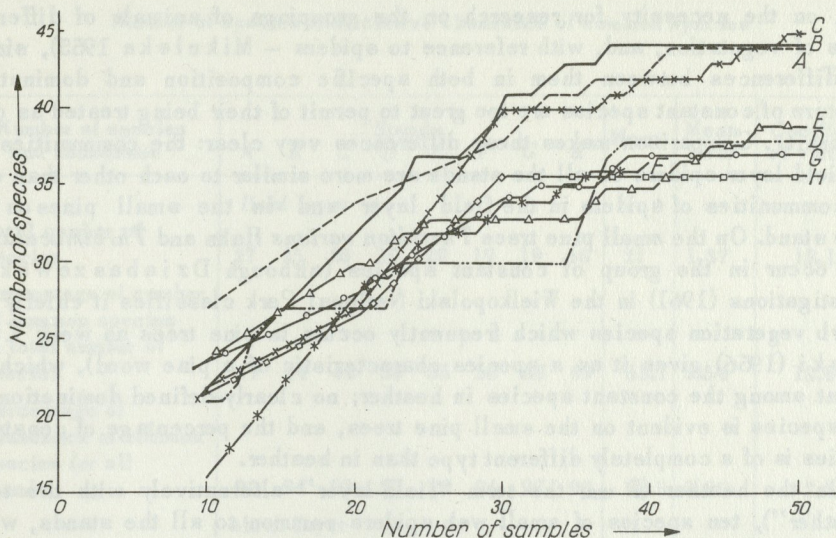


Fig. 2. Curves of increase in the number of species of small web spiders in the field layer together with an increase in the number of samples (data from 1959)  
Stands A - H

The distribution of species on stand A would seem to be considerably more uniform than on stand B, and in particular on stand C. On stand A 96% of the species occurring in 50 samples had been caught by the 26th sample. The distribution of species on stand C seems to be not uniform ("step-shaped" shape of the curve); new species continually appear.

As regards the level of number of species the communities of small web spiders on all stands can be divided into two groups. One of these groups includes communities on stands A, B, C (the oldest pine trees), which are characterised by a larger number of species (26, 24, 23), the second includes the communities on stands D, E, F, G, H (younger pine trees) which have a smaller number of species (17, 18, 18, 17, 14) (Fig. 2).

Thus an analysis of all species of spiders (Fig. 1) and of small web spiders only (Fig. 2) shows that as regards the number of species the communities of the 8 stands examined may be divided into two groups: the communities of the older stands (A, B, C) with a larger number of species and the communities of the younger stands (D, E, F, G, H) possessing a smaller number.

## STRUCTURAL CHARACTERISTICS OF SPIDER COMMUNITIES

### 1. Specific composition

The communities of spiders in the field layer and small pine trees on each stand have been considered separately (see, inter alia, Elton and Miller



1954, on the necessity for research on the groupings of animals of different layers of vegetation, and, with reference to spiders – Mikulska 1955), since the differences between them in both specific composition and domination structure of constant species are too great to permit of their being treated as one community. Comparison makes these differences very clear: the communities of the field layer spiders on all the stands are more similar to each other than are the communities of spiders in the field layer and in the small pines on the same stand. On the small pine trees *Theridion varians* Hahn and *Th. bimaculatum* (L.) occur in the group of constant species (although Dziabas zewski's investigations (1961) in the Wielkopolski National Park classifies it chiefly as a herb vegetation species which frequently occurs in pine trees as well; Karpinski (1956) gives it as a species characteristic of a pine wood), which is absent among the constant species in heather; no clearly-defined domination of one species is evident on the small pine trees, and the percentage of constant species is of a completely different type than in heather.

On the heather (I use the term "field-layer" alternatively with the term "heather"), ten species of small web spiders common to all the stands, were found. The number of common species is, depending on the stand, from 41 to 69% of all the species collected (Tab. III). These species are as follows: of the *Argiopidae*: *Araneus cucurbitinus* Cl., *A. redii* (Scop.), *A. quadratus* Cl., *A. diadematus* Cl., *Mangora acalypha*. The predominant species among these is *Mangora acalypha*, and the remainder are represented by a few specimens only; of the *Dictynidae* – *Dictyna arundinacea* (L.), subdominant and influent; of the *Theridiidae* – *Theridion simile* C. L. Koch and *Th. sisyphium* (Cl.); of the *Linyphiidae* – *Linyphia pusilla* Sund.; of the *Tetragnathidae* – *Tetragnatha pinicola* L. Koch.

The following species belonging to medium-sized web spiders were found, on all stands – *Linyphia triangularis* (Cl.) and on seven stands – *Araneus adiantus* (Walck.).

Nine common species were found in the small pine tree layer (shrub layer) on all the stands. These are: *Araneus cucurbitinus*, *A. diadematus*, *Mangora acalypha*, *Tetragnatha pinicola*, *Theridion simile*, *Th. varians*, *Th. sisyphium*, *Th. bimaculatum*, *Linyphia pusilla*. Seven of these species belong to species common to both – field layer and shrub layer. The percentage constituted by the number of common species in relation to the total number of species captured on the different stands is from 36 to 60% (Tab. III). The same species occur in the layer of small pine trees as in the field layer; only three species were captured which do not occur on heather: *Ero tuberculata* – 1 specimen, *Erigoninae* gen. sp. – 2 individuals and *Theridion lunatum* (Cl.) – 1 individual.

As will be seen from the above, the communities in the heather layer and small pine tree layer are similar to each other, if we take into consideration the whole specific composition of the communities, and not constant species (common to all the stands).

Species common to all stands (constant species) determine the character and abundance of all definite communities. They are the chief components of



Number of species and relative abundance of common species

Tab. III

Number of species and abundance	Stands								Mean	Mean error	Coefficient of variation
	A	B	C	D	E	F	G	H			
	field layer										
Total number of species	27	25	26	19	20	19	19	16	21	1.37	18.13
Percentage of number of common species in total number of species	41	44	42	58	55	58	58	69	53.1	3.54	18.86
Percentage of abundance of common species for all stands	90	94	93	97	93	94	97	98	94.5	0.95	2.83
	shrub layer										
Total number of species	21	20	22	19	23	20	17	15			
Percentage of number of common species in total number of species	37	45	47	41	36	45	53	60	45.5	2.84	17.66
Percentage of abundance of common species for all stands	76	75	82	90	78	84	93	91	83.6	1.65	8.85

spider communities (Tab. III). On these grounds it is possible to find the existence of the same association of small web spiders on all stands in the field layer and a slightly different association on small pine trees.

#### FIELD LAYER

The greatest numbers of web species on the heather (27, 26, 25) were caught on the stands where the oldest pine trees grow (stands A, B, C), from 16 to 20 species being caught on the remaining five younger stands (Tab. IV, V). In the pine tree layer no correlation between the number of species and the age of the pine trees was discovered. In both layers the smallest number of web spiders occurs in the "hollow" (area H - 16 and 15 species).

The presence of *Dipoena tristis* Hahn (areas A, B, C), *Zilla diodia* Walck. (A, C), *Cyclosa conica* Pall. (A, B), *Cercidia prominens* Westr. (A, C) which occurred only on older stands, is characteristic; two of them are hemiombriophiles, 2 hylobionts (inhabitants of forests, both in the sunlit and shady parts, Tretzel 1952).



Abundance of small web spiders in the field layer during the period from August to September 1959

Tab. IV

Species	Stands								Mean	Mean error	Coefficient of variation
	A	B	C	D	E	F	G	H			
<i>Araneus cucurbitinus</i> Cl.	8	11	7	13	15	12	10	5			
<i>Araneus redii</i> (Scop.)	2	5	8	5	12	9	6	12			
<i>Araneus quadratus</i> Cl.	1	9	6	7	9	6	1	5			
<i>Araneus patagiatus</i> Cl.		2			1	3	2	1			
<i>Araneus marmoreus</i> Cl.	1										
<i>Araneus sturmi</i> (Hahn)	4	1	1	1	3	6					
<i>Araneus diadematus</i> Cl.	1	2	2		4	1	2	4			
<i>Araneus umbraticus</i> Cl.			1		1						
<i>Araneus marmoreus</i> f. <i>pyr.</i> Cl.	1										
<i>Aranus</i> sp.		2	1			1	1				
<i>Mangora acalypha</i> (Walck.)	640	279	240	186	140	130	133	148	237	60,71	72,45
<i>Singa pygmaea</i> (Sund.)		6	4			1	1	1			
<i>Zilla diodia</i> (Walck.)	1		1								
<i>Cyclosa conica</i> (Pall.)	4	2									
<i>Meta segmentata</i> (Cl.)		1									
<i>Cercidia prominens</i> (Westr.)	1		1								
<i>Singa hamata</i> (Cl.)			1								
<i>Tetragnatha pinicola</i> L. Koch	37	20	7	8	7	8	8	8	12,9	3,77	82,96



<i>Tetragnatha obtusa</i> C. L. Koch	1		1		6	1	1				
<i>Dictyna arundinacea</i> (L.)	196	236	76	76	21	22	19	4	81.3	31.1	108.25
<i>Theridion simile</i> C. L. Koch	47	45	15	16	52	48	16	7	30.7	6.63	61.01
<i>Theridion varians</i> Hahn	27	6	3	1		4	1				
<i>Theridion sisypium</i> (Cl.)	4	9	8	4	25	17	18	8	11.6	2.66	64.75
<i>Theridion bimaculatum</i> (L.)	6		3	2	1		1				
<i>Theridion pinastri</i> L. Koch	3	2			2						
<i>Theridion tinctum</i> (Walck.)	1						1				
<i>Theridion</i> sp.	1										
<i>Dipoena</i> sp.	2	3	1								
<i>Linyphia pusilla</i> Sund.	65	16	22	5	14	7	8	19	19.5	6.84	99.17
<i>Gonatium rubens</i> (Blackw.)	17	4	8	2	4			1			
<i>Lepthyphantes tenuis</i> (Blackw.)		1									
<i>Erigone dentipalpis</i> (Wider)				1							
<i>Linyphiidae</i> gen. sp.	11	7	3	2	6						
<i>Ero aphana</i> (Walck.)			1								
<i>Ero furcata</i> (Villers)				1							
<i>Ero</i> sp.	25	6		1			1	2			
Total	1110	675	420	331	323	277	229	225	448.8	107.44	67.71



Abundance of small web spiders in the shrub layer during the period from August to September 1959

Tab. V

Species	Stands								Mean	Mean error	Coefficient of variation
	A	B	C	D	E	F	G	H			
<i>Araneus cucurbitinus</i> Cl.	15	15	10	22	25	18	15	4	15.5	2.32	42.37
<i>Araneus redii</i> (Scop.)			5		3	3	3				
<i>Araneus quadratus</i> Cl.		3	1	3	2			1			
<i>Araneus adiantus</i> (Walck.)			4	1		1		2			
<i>Araneus sturmi</i> (Hahn)	8	5	4	2	5	7					
<i>Araneus diadematus</i> Cl.	2	2	2	3	8	1	4	3			
<i>Araneus marmoreus</i> Cl.	1	1		1	1						
<i>Araneus patagiatus</i> Cl.	2	3		2	2	1	1				
<i>Araneus umbraticus</i> Cl.	1										
<i>Mangora acalypha</i> (Walck.)	77	38	16	22	25	48	21	17	33	7.39	63.36
<i>Cyclosa conica</i> (Pall.)	4	3		1							
<i>Singa</i> sp.					1						
<i>Zilla diodia</i> (Walck.)						1					
<i>Dictyna arundinacea</i> (L.)	7	14	5	2	1						
<i>Tetragnatha pinicola</i> L. Koch	3	3	2	2	3	2	5	6			



<i>Tetragnatha obtusa</i> C. L. Koch	3			1	3	1	1	1			
<i>Theridion simile</i> C.L. Koch	19	15	12	14	30	58	23	2	21.6	5.95	77.87
<i>Theridion varians</i> Hahn	84	25	13	14	9	7	4	1	19.6	9.55	137.75
<i>Theridion sisyphium</i> (Cl.)	4	21	20	18	33	35	35	23	23.6	3.75	44.86
<i>Theridion bimaculatum</i> (L.)	7	2	1	1	4	3	3	3			
<i>Theridion pinastri</i> L. Koch	2		1	1	7	7	2				
<i>Theridion tinctum</i> (Walck.)	8	2	1	2	8	9					
<i>Theridion lunatum</i> (Cl.)			1								
<i>Dipoena</i> sp.		2	1	1	1	3					
<i>Linyphia pusilla</i> Sund.	5	1		1	1	2	2	3			
<i>Linyphia triangularis</i> (Cl.)	7	2	7	4	1		1	1			
<i>Leptyphantes</i> sp.							1				
<i>Erigoninae</i> gen. sp.							1				
<i>Linyphiidae</i> gen. sp.	8	6	2	2	4	2	1	1			
<i>Ero</i> sp.	26	5	1		1	1		2			
<b>Total</b>	<b>294</b>	<b>168</b>	<b>105</b>	<b>120</b>	<b>180</b>	<b>210</b>	<b>123</b>	<b>70</b>			
<b>Only small web spiders</b>	<b>285</b>	<b>162</b>	<b>93</b>	<b>108</b>	<b>177</b>	<b>208</b>	<b>120</b>	<b>68</b>	<b>153</b>	<b>25</b>	<b>16.41</b>



Of the seven species caught only on one stand, six were found on older stands. There were no species characteristic only of the younger stages of the pine plantation.

In order to compare the specific composition of the stands examined in greater detail, calculation was made of the index of specific similarity according to Sørensen (1948). This index is calculated for two definite communities, dividing the double number of common species ( $c$ ) by the sum total of number of species occurring in each community ( $a, b$ ), according to formula  $QS = \frac{2c}{a+b}$ ; the result is multiplied by 100, obtaining the numerical index in percentages. The higher the value of the index, the greater the similarity of specific composition.

Index of specific similarity in the communities of web spiders of the field layer

Tab. VI

A, B	73	B, A	73	C, A	79	D, A	74
A, C	79	B, C	78	C, B	78	D, B	77
A, D	74	B, D	77	C, D	80	D, C	80
A, E	72	B, E	75	C, E	78	D, E	82
A, F	65	B, F	77	C, F	75	D, F	74
A, G	65	B, G	77	C, G	80	D, G	79
A, H	60	B, H	78	C, H	71	D, H	80
60-79		73-78		71-80		74-82	
E, A	72	F, A	65	G, A	65	H, A	60
E, B	75	F, B	77	G, B	77	H, B	78
E, C	78	F, C	75	G, C	80	H, C	71
E, D	82	F, D	74	G, D	79	H, D	80
E, F	77	F, E	77	G, E	77	H, E	78
E, G	77	F, G	89	G, F	89	H, F	80
E, H	78	F, H	80	G, H	86	H, G	86
72-82		65-89		65-89		60-86	

The index fluctuates within limits of 60-89% for all the pairs of communities in the field layer (Tab. VI, fig. 3). The fairly high index of from 75 to 80 is most frequently repeated, indicating considerable general similarity of specific composition in the majority of communities. This general similarity must be the more strongly emphasised since species which do not occur on all stands, and in particular species found only on one or two stands, are in the majority species represented by very small numbers of individuals. Thus the differences in the index are chiefly caused by rare species, which play a very small part in the community, yet despite this the indices are high. As an example it is worth quoting that with Sørensen (1948) the amplitude of the indices is from 22 to 80, with Haarlov (1960) 20-79, while in the present study they are from 60-89.

All these communities, very similar to each other, may be divided into three groups, composed of communities most similar from the aspect of specific com-



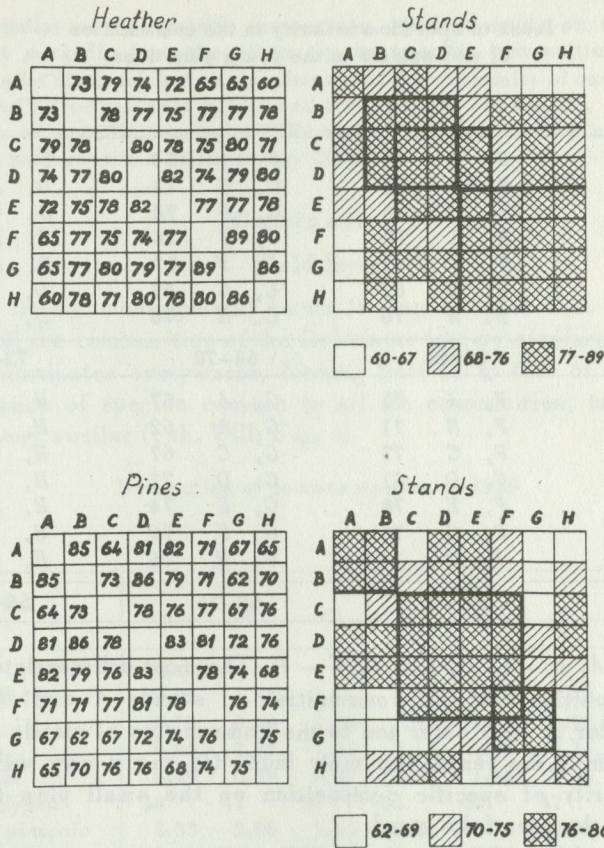


Fig. 3. Index of specific similarity (QS) in the field layer and the shrub layer on young pine trees (data from 1959)

position. These are; A - B, C, D - E, F, G, H. The most similar pairs of communities come from stands G and F and G and H (QS is high: 89, 86). The lowest indices are obtained when comparing communities of spiders on stand A with others, and in particular with the community from stand H (60).

From the above description it will be seen that the similarity of specific composition is to a very great extent correlated with the age of the wood on the study area, and to a far lesser degree with differences in the plant associations (Tab. I).

### Shrub layer

In the communities of web spiders of the upper layer (small pine trees) the index varies within limits of 62-86 (Tab. VII, Fig. 3). Four groups can be



Index of specific similarity in the communities  
of web spiders in the young pine trees

Tab. VII

<i>A, B</i> 85	<i>B, A</i> 85	<i>C, A</i> 64	<i>D, A</i> 81
<i>A, C</i> 64	<i>B, C</i> 73	<i>C, B</i> 73	<i>D, B</i> 86
<i>A, D</i> 81	<i>B, D</i> 86	<i>C, D</i> 78	<i>D, C</i> 78
<i>A, E</i> 82	<i>B, E</i> 79	<i>C, E</i> 76	<i>D, E</i> 83
<i>A, F</i> 71	<i>B, F</i> 71	<i>C, F</i> 77	<i>D, F</i> 81
<i>A, G</i> 67	<i>B, G</i> 62	<i>C, G</i> 67	<i>D, G</i> 72
<i>A, H</i> 65	<i>B, H</i> 70	<i>C, H</i> 76	<i>D, H</i> 76
64-85	62-86	64-78	72-86
<i>E, A</i> 82	<i>F, A</i> 71	<i>G, A</i> 67	<i>H, A</i> 65
<i>E, B</i> 79	<i>F, B</i> 71	<i>G, B</i> 62	<i>H, B</i> 70
<i>E, C</i> 76	<i>F, C</i> 77	<i>G, C</i> 67	<i>H, C</i> 76
<i>E, D</i> 83	<i>F, D</i> 81	<i>G, D</i> 72	<i>H, D</i> 76
<i>E, F</i> 78	<i>F, E</i> 78	<i>G, E</i> 74	<i>H, E</i> 68
<i>E, G</i> 74	<i>F, G</i> 76	<i>G, F</i> 76	<i>H, F</i> 74
<i>E, H</i> 68	<i>F, H</i> 74	<i>G, H</i> 75	<i>H, G</i> 75
74-83	71-81	62-76	65-76

distinguished: *A, B* - *C, D, E* - *F, G* - *H*. The most differentiated as regards specific composition are the communities of stands *A* and *B*, which are extremely similar to each other and to the communities of stands *D* and *E* and greatly differ from the remainder; their index *QS* has a very wide amplitude.

The similarity of specific composition on the small pine trees is also correlated with the age of the stand.

The indices of specific similarity differentiate the communities of spiders in the field layer and shrub layer in a different way. On the heather the community of stand *A* differed most from all the others, while on the small pine trees the community of stand *A* is similar to the communities on stands *B, D* and *E*. The communities of spiders on the pine trees on stands *G* and *H* differ greatly from each other and from the remainder, and the communities of the field layer of stands *G* and *H* (stand surrounded by dunes) are very similar to each other. It may be assumed that the neighbourhood of the dunes renders the specific composition in the lower layer more uniform, and affects to a lesser extent the community of the pine tree layer.

To sum up:

1. The specific composition is very similar on all stands (high *QS* indices) (Tab. IV, V, VI, VII, Fig. 3).
2. Ten species common to all the stands occur in the field layer, nine on the pine trees; they belong to 5 families.
3. In the field layer on the older stands, more species occur than on the younger stands (Tab. III, Figs. 1 and 2); there is no correlation between the number of species and the age of the stand in the pine trees (shrub layer).
4. According to the index of specific similarity 3 variants can be distinguished in the



field layer, similar as to specific composition, the community on the oldest stand deviating most markedly from the others by its specific composition; 4 variants of association can be distinguished on the pine trees; the community of one of the youngest stands ("hollow") diverges most from the others (Tab. VI, VII, Fig. 3).

5. The indices of specific similarity differentiate the communities of spiders in the field layer and pine trees in a different way (Fig. 3).

### Domination

#### Field layer

Speaking in the most general terms it may be said that the domination structure in all the communities of the field layer is very similar; in 1959 *Mangora acalypha* dominates everywhere, forming from 41 to 66% of the community. The participation of species common to all the communities, taken jointly, is everywhere very similar (Tab. VIII, Fig. 4)

#### Domination of common species in 1959

Tab. VIII

Species	Stands							
	A	B	C	D	E	F	G	H
field layer								
<i>Araneus cucurbitinus</i>	0.72	1.63	1.66	3.90	4.64	4.33	4.36	2.22
<i>A. redii</i>	0.18	0.74	1.90	1.51	3.71	3.25	2.62	5.40
<i>A. quadratus</i>	0.09	1.33	1.42	2.11	2.78	2.16	0.43	2.22
<i>A. diadematus</i>	0.09	0.30	0.47	0.60	1.23	0.36	0.87	1.77
<i>Mangora acalypha</i>	58	41	57	56	43	47	58	66
<i>Tetragnatha pinicola</i>	3.33	2.96	1.66	2.41	2.16	2.88	3.49	3.55
<i>Dictyna arundinacea</i>	17.66	35	18	23	6.50	7.94	8.30	1.78
<i>Theridion simile</i>	4.23	6.66	3.57	4.83	16.09	17.32	7	3.11
<i>Th. sisyphium</i>	0.36	1.33	1.90	1.20	7.74	6.13	3.55	7.86
<i>Linyphia pusilla</i>	5.85	2.37	5.23	1.51	4.33	2.52	8.44	3.49
Total percent about	90	93	93	97	92	94	97	97
shrub layer								
<i>Araneus cucurbitinus</i>	5.26	9.26	10.75	19.45	14.79	8.65	12.93	6.15
<i>Mangora acalypha</i>	27.01	23.45	17.20	20.37	14.79	23.07	18.10	26.15
<i>Tetragnatha pinicola</i>	1.05	1.85	2.15	1.85	1.77	0.96	4.31	9.23
<i>Theridion simile</i>	6.66	9.26	12.90	12.96	17.75	27.88	19.81	3.07
<i>Th. varians</i>	29.47	15.43	13.97	12.96	5.32	3.36	3.44	1.53
<i>Th. sisyphium</i>	1.40	12.50	21.50	16.66	19.52	16.92	30.17	35.38
<i>Th. bimaculatum</i>	2.45	1.23	1.07	0.92	2.36	1.44	2.58	4.61
<i>Linyphia pusilla</i>	1.75	0.61		0.92		0.96	1.72	4.01
Total percent about	75	74	80	86	76	83	93	90

Differentiation of the predominant species has been based in this study on the principle used by Renkonen (1938) for distinguishing the dominant. This scientific worker considers that predominant species cannot be distinguished



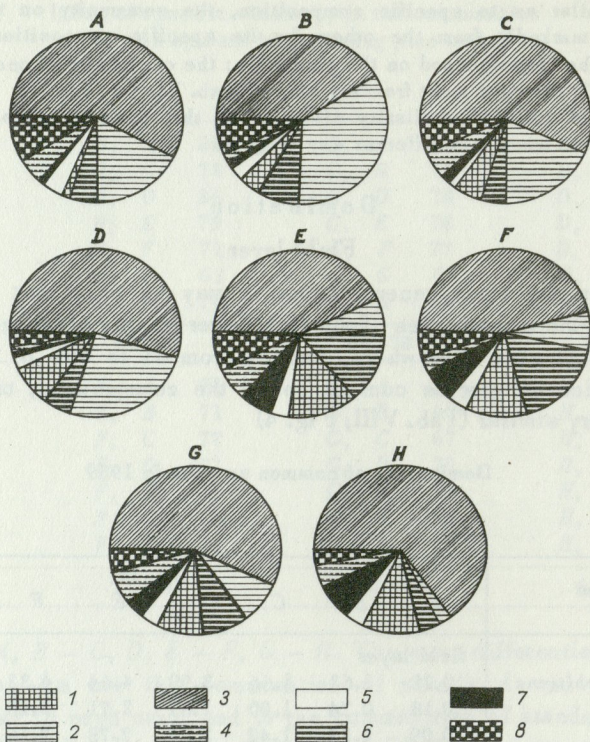


Fig. 4. Domination relations of small web spiders in the field layer in 1959  
 1 - *Araneus* sp., 2 - *Dictyna arundinacea*, 3 - *Mangora acalypha*, 4 - *Linyphia pusilla*, 5 -  
*Tetragnatha pinicola*, 6 - *Theridion simile*, 7 - *Th. sisyphium*, 8 - other species

according to a pre-established value of degree of domination of a species in the community (e.g. species forming 5% of the community should be classified as dominants), but according to the differences in abundance found in the respective material, e.g. according to the gap separating the predominant species from the next most numerous species. In the present work the dominant species occurred in 1959 in numbers greater than 40% of the total numbers of spiders in the community; the influent species following in order of abundance had domination values from 16–23%. There is a considerable gap between influent and accessory species (influents 16–23%, accessory species below 8%).

If the domination structure is analysed in greater detail, calculating the percentages of each species, then differences, secondary but clearly-defined, can be observed between the communities.

The similarity of domination of species of two definite communities (the so-called Renkonen number -  $Re$ ) is calculated by totalling the lesser values of domination of common species. For example, species  $X$  on stand  $A$  forms



80% of the community, and on stand *B* – 60%; species *Y* is 20% on stand *B*, and on stand *A* – 50%. The values 60 and 20 are added. The sum of all the lesser values of domination of common species is an index of similarity of the two communities compared.

In the communities in the field layer the index of similarity of domination takes on values from 57 – 87 (Tab. IX, Fig. 5).

Index of similarity of domination in communities  
of web spiders in the field layer

Tab. IX

<i>A, B</i> 70	<i>B, A</i> 70	<i>C, A</i> 87	<i>D, A</i> 83
<i>A, C</i> 87	<i>B, C</i> 72	<i>C, B</i> 72	<i>D, B</i> 78
<i>A, D</i> 83	<i>B, D</i> 78	<i>C, D</i> 87	<i>D, C</i> 87
<i>A, E</i> 62	<i>B, E</i> 65	<i>C, E</i> 67	<i>D, E</i> 68
<i>A, F</i> 66	<i>B, F</i> 67	<i>C, F</i> 70	<i>D, F</i> 73
<i>A, G</i> 78	<i>B, G</i> 66	<i>C, G</i> 81	<i>D, G</i> 81
<i>A, H</i> 73	<i>B, H</i> 57	<i>C, H</i> 75	<i>D, H</i> 73
62 87	57 – 78	67 – 87	68 – 87
<i>E, A</i> 62	<i>F, A</i> 66	<i>G, A</i> 78	<i>H, A</i> 73
<i>E, B</i> 65	<i>F, B</i> 67	<i>G, B</i> 66	<i>H, B</i> 57
<i>E, C</i> 67	<i>F, C</i> 70	<i>G, C</i> 81	<i>H, C</i> 76
<i>E, D</i> 68	<i>F, D</i> 73	<i>G, D</i> 81	<i>H, D</i> 73
<i>E, F</i> 87	<i>F, E</i> 87	<i>G, E</i> 78	<i>H, E</i> 68
<i>E, G</i> 78	<i>F, G</i> 81	<i>G, F</i> 81	<i>H, F</i> 69
<i>E, H</i> 68	<i>F, H</i> 69	<i>G, H</i> 80	<i>H, G</i> 80
62 – 87	66 – 87	66 – 81	57 – 80

A characteristic feature of domination relations in spider communities on the stands examined is the lack of distinct correlation with all the features distinguished of the given stands; other indices (*QS* and *Ku*) exhibit distinct correlation with the age of the pine trees, while the index of similarity of domination exhibits it to a far smaller degree: communities *E* and *F* like *G* and *H* are similar (both pairs are rendered similar by the age of the pine trees) but the communities of stands *A, C, D, G* also form a similar group, despite the fact that the stands differ greatly as to age. This suggests that the phenomenon of domination is not strictly subject to the regularities the index of which is the age of the small pine trees; other factors must play a part here, possibly competition relations for food and space between the species of the community ecologically similar to each other. Many ecologists (Chapman 1931, Renkonen 1938, Lityński 1938) consider domination structure as resulting from competition.

Detailed analysis of the domination structure of species revealed differences in the communities even at the level of the influent. *Dictyna arundinacea* is a co-dominant on area *B*, an influent on three stands *A, C, D* (18%, 19%, 23%), that is on older stands, and *Theridion simile* is an influent on stands *E* – 17% and *F* – 17%. There is no influent on the remaining two youngest stands.



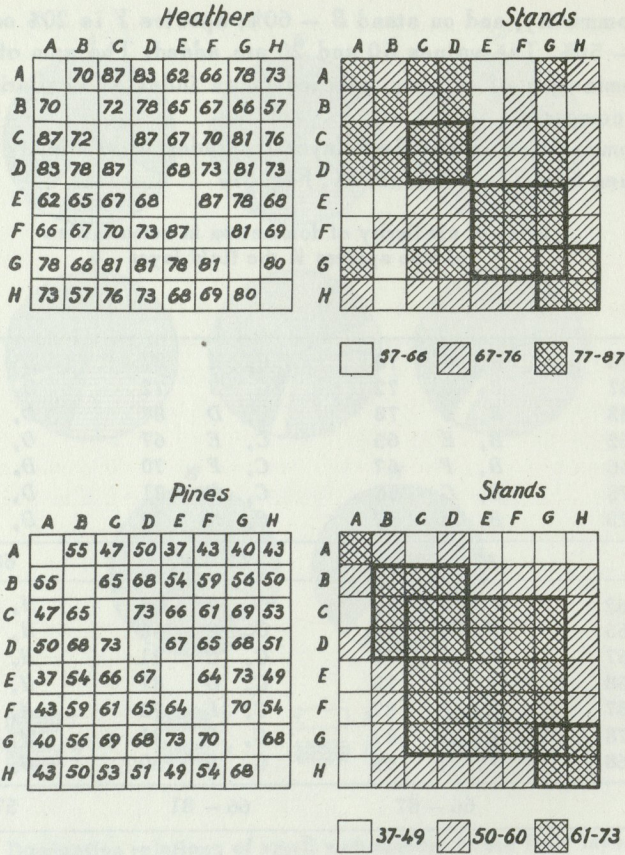


Fig. 5. Index of similarity of domination ( $R_e$ ) of species of spiders occurring in the field layer and on the shrub layer in 1959

In the communities of small web spiders in the field layer several types of domination can be distinguished: (Tab. IX, Fig. 5) B – D, C, A – E, F – G, H.

1. Community on stand B has the lowest degree of domination of *Mangora acalypha* (41%) and the highest of *Dictyna arundinacea* (35%). It is very similar to the community on stand A as regards other characters.

2. The group from stands D, C and A is characterised by the same domination of *Mangora acalypha* (56%, 57%, 57%), a similar percentage of *D. arundinacea* (23%, 18%, 17%) and *Theridion simile* (5%, 3.5%, 4%). The community on stand A has the lowest percentage, in relation to the others, of species of the genus *Araneus* and *Th. sisypium*, the community on stand D has a larger percentage of *D. arundinacea* than the two remaining ones.

3. The communities of stands E and F, exhibit an almost identical domination structure: there is a far smaller percentage of *D. arundinacea* (6.5%



and 7.9%) and a greater percentage of species of the genus *Araneus* and *Th. sisyphium*.

4. The communities on stands *G* and *H* are also similar to each other: there is a large percentage of individuals of the genus *Araneus*, a similar percentage of *Tetragnatha pinicola* and *Theridion sisyphium*. *D. arundinacea* and *Linyphia pusilla* are represented on stand *H* by a very small percentage.

### Shrub layer

A feature distinguishing the domination structure of web spider community in pine trees from the same structure on the heather is the lack on the majority of the stands of distinct domination by one or two species. It is impossible to distinguish a predominant species on account of the absence of a large gap between percentages of domination of each of the more numerous species. Several species (4 to 5) have a medium percentage in the community (12% – 23%), the remainder – a very small one (Tab. VIII, Fig. 6). The following species, which are also numerous in the field layer, belong among the more numerous

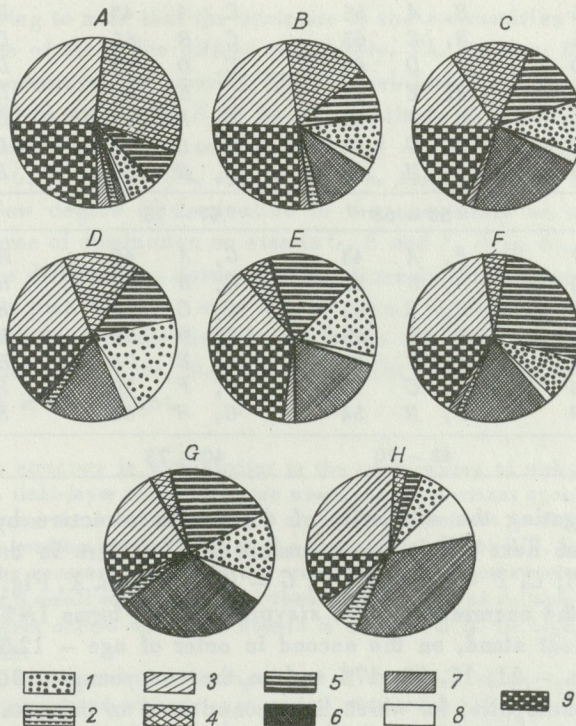


Fig. 6. Domination relations in small web spiders on the shrub layer in 1959

1 – *Araneus cucurbitinus*, 2 – *Linyphia pusilla*, 3 – *Mangora acalypha*, 4 – *Theridion varians*, 5 – *Th. simile*, 6 – *Th. sisyphium*, 7 – *Th. bimaculatum*, 8 – *Tetragnatha pinicola*, 9 – other species



species — *M. acalypha*, *Th. simile*, *Th. sisyphium* (this last species is far more abundant in the pine trees) (Fig. 6), while *Araneus cucurbitinus* and *Theridion varians* (Locket and Millidge 1953, Dziabas zewski 1961) are characteristic of the shrub layer. Only stands *A* and *H* (the oldest and one of the youngest) differ, having two species each with a far higher percentage in the community than the others. On stand *A* these species are *M. acalypha* and *Th. varians*, on stand *H* — *M. acalypha* and *Th. sisyphium*. As can be seen, the oldest pine plantation has a dominant characteristic of the shrub layer (*Th. varians*), which however shares domination with a field layer species. Intensive occupation of the higher layer of vegetation by a species dominant in the field layer is evident on all the stands, but only on the oldest are relations formed into a distinct domination structure similar to that in field layer — the dominant is a species characteristic of the given layer.

Index of similarity of domination in communities  
of web spiders in the shrub layer

Tab. X

<i>A, B</i> 55	<i>B, A</i> 55	<i>C, A</i> 47	<i>D, A</i> 50
<i>A, C</i> 46	<i>B, C</i> 65	<i>C, B</i> 65	<i>D, B</i> 68
<i>A, D</i> 50	<i>B, D</i> 68	<i>C, D</i> 73	<i>D, C</i> 73
<i>A, E</i> 37	<i>B, E</i> 54	<i>C, E</i> 66	<i>D, E</i> 67
<i>A, F</i> 43	<i>B, F</i> 59	<i>C, F</i> 61	<i>D, F</i> 65
<i>A, G</i> 40	<i>B, G</i> 56	<i>C, G</i> 69	<i>D, G</i> 68
<i>A, H</i> 43	<i>B, H</i> 50	<i>C, H</i> 53	<i>D, H</i> 51
40 — 55	50 — 68	47 — 73	50 — 68
<i>E, A</i> 37	<i>F, A</i> 43	<i>G, A</i> 40	<i>H, A</i> 43
<i>E, B</i> 54	<i>F, B</i> 59	<i>G, B</i> 56	<i>H, B</i> 50
<i>E, C</i> 66	<i>F, C</i> 61	<i>G, C</i> 69	<i>H, C</i> 53
<i>E, D</i> 67	<i>F, D</i> 65	<i>G, D</i> 68	<i>H, D</i> 51
<i>E, F</i> 64	<i>F, E</i> 64	<i>G, E</i> 73	<i>H, E</i> 49
<i>E, G</i> 73	<i>F, G</i> 70	<i>G, F</i> 70	<i>H, F</i> 54
<i>E, H</i> 49	<i>F, H</i> 54	<i>G, H</i> 68	<i>H, G</i> 68
37 — 73	43 — 70	40 — 73	43 — 68

In investigating the similarity of domination structure by the Renkonen method, we can next divide the communities of spiders in the pine trees as follows: *A* — *B*, *C*, *D* — (*C*, *D*) *E*, *F*, *G* — (*G*), *H* (Tab. X, Fig. 5). Particularly interesting is the occurrence of *Th. sisyphium* which forms 1.4% of the community on the oldest stand, on the second in order of age — 12.5%, on the intermediate stands — 21, 17, 20, 17% and on the two youngest 30 and 35%. This species is a photophile, for which light constitutes an important factor deciding its distribution; it settles in shadier stands (older ones) to a far lesser degree. The second species, the percentage of which in the community varies considerably, is *Th. varians*, which is distributed in a completely opposite way to the first species, i.e. more densely on old stands, the third is *Th. simile*,



with values of percentage in the community not correlated (similarly to the situation in the field layer) with the age of the stand.

The index of similarity of domination takes on values from 36.8% to 73% (Tab. X, Fig. 5).

The community on stand *A* is distinguished by the lowest indices of similarity of domination (40–55%), and therefore is the least similar to other communities. The most abundant species are *Th. varians* (29.5%) and *M. acalypha* (27%), and the six following common species (*Th. simile*, *Th. sisymphium*, *Th. bimaculatum*, *A. cucurbitinus*, *T. pinicola*, *L. pusilla*) do not form, even taken together, 20% of the community.

The communities of stands *B*, *C*, *D* have similar percentages for *M. acalypha*, *Th. varians* and *Th. simile*, stand *B* is distinguished by a greater percentage of other species (apart from the common species), *D* – by the percentage of *A. cucurbitinus*, *C* – by percentage of *Th. sisymphium*.

The communities on *E*, *F* and *G* have similar percentages of domination, although *F* is distinguished by a higher percentage of *Th. simile*, and *G* – by the considerably greater participation of *Th. sisymphium* from which aspect it is similar to the community on stand *H*.

It is interesting to note that the structure in the communities most unlike as regards the value of the index differs completely. *Th. varians*, the predominant species in the community on stand *A* (29.5%), exhibits its lowest values (3.4%, 5.3%, 1.5%, 3.3%) on stands *G*, *E*, *H* and *F*. Similarly *M. acalypha*, the highest degree of dominance of which occurs on stand *A* (27%), exhibits its lowest values on stand *G*, *D* and *E*. *Th. simile* and *Th. sisymphium*, on the other hand, which have a low degree of domination in the community on stand *A*, attain their highest degree of domination on stands *G*, *E* and *F*. (Fig. 6).

Despite these differences, domination relations in the communities of small web spiders in the pine trees are more similar among themselves than they are to the domination relations in the field layer. It can also be seen here, even more clearly than in the field layer, that the correlation of domination relations with age of the stands is very slight.

To sum up:

1. The domination structure is very similar in the communities of web spiders, both of those living in the field-layer and in the pine trees; the predominant species *M. acalypha* occurs everywhere on the heather; there is no distinct dominant in the pine trees, but 4–5 species form a medium participation in the communities (Tab. VIII, Fig. 6).
2. Individuals of the constant species in the communities (common species) form 90–98% of the numbers of all small web spiders; on these grounds it was accepted that the same association of spiders occurs on all the stands in each layer in the type of environment examined (Tab. VIII).
3. The variants of the association distinguished on the basis of the index of similarity of domination are correlated with the age of the pine trees to a considerably slighter extent than the variants distinguished on the basis of similarity of species and of similarity of abundance (Tab. IX, X, Fig. 5).



## Constancy

The frequency of the species measured by its presence in samples, or in series of samples (the ratio of number of samples containing this species to the number of all samples taken, times 100) is one of the characters of the community which is used in plant sociology when comparing communities of different stands in one biotope. The index of frequency depends on the way in which the individuals of the species are distributed in the area and their abundance, and on this account is not ecologically too clear; but as it contains in itself information as to two important ecological properties of the species (numbers and distribution) it can play the part of an index of the character of occurrence of the species in the environment examined, particularly when comparing similar communities. Comparison of indices of frequency in two communities gives the index of similarity of constancy.

The index of similarity of constancy can be calculated in a different way. Kulczyński (1928) calculated it for different plant associations on the basis of the occurrence of the species in different patches of vegetation of the same type. In the present work the frequency in the samples of individuals of each species common to all the stands (constant species in the community) was used as a basis. The percentage of frequency in samples from one stand was converted into the number 1-5 according to the known scale of constancy:

Frequency of species	Scale of constancy
100-80	5
80-60	4
60-40	3
40-20	2
20-1	1

and set to the formula (Kulczyński 1928)

$$Ku = \frac{\frac{c}{a} + \frac{c}{b} \cdot 100}{2}$$

where  $a$  is the sum of the values of frequency of species in one community,  $b$  - the sum of values of frequency in a second community and  $c$  - the sum of values common to both communities.

Example:	Common species	Community A	Community B	Common value of frequency
	Species X	4	3	3
	Species Y	5	2	2
	Species Z	-	1	-
		$a = 9$	$b = 6$	$c = 5$



$$Ku = \frac{5}{9} + \frac{5}{6} \cdot \frac{100}{2} = (0.56 + 0.83) \cdot \frac{100}{2} = \frac{139}{2} = 69.5$$

The limit of the index is 100. The greater the index, the greater the similarity of constancy. This index is the similarity of frequency of common species; it is calculated separately for each pair of stands examined.

According to the index of similarity of constancy (Fig. 7) the areas on which frequency of species is similar, can be arranged in order as follows; A - B, C,

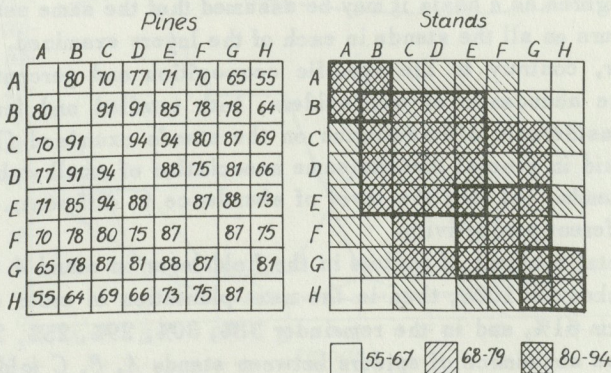
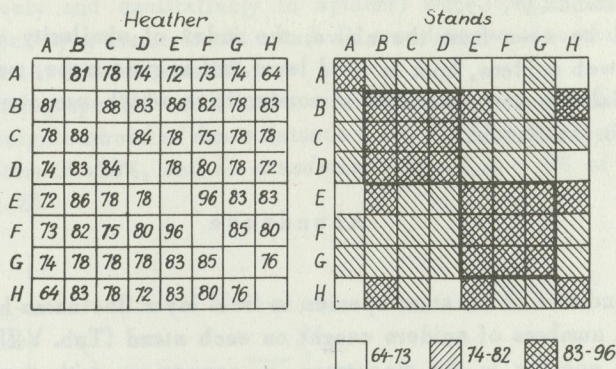


Fig. 7. Index of similarity of constancy ( $Ku$ ) of species of spiders occurring in the field layer and on the shrub layer in 1959

D - E, F, G - H. Apart from communities H and A (which is similar only to B) we can distinguish two groups of similar communities of spiders. Similarity of constancy falls into a pattern according to the classification of stands into older and younger. Such results, as in the case of consideration of abundance of species on stands, should not be considered surprising, if the connection between frequency and abundance (Greig-Smith 1957) is remembered.



Apart from the common species the greatest frequency on stand *A* is exhibited by such species as *Th. varians*, *Gonatium rubens* (Blackw.) and species of the genus *Ero*. *Dipoena tristis* exhibits the greatest frequency on stand *B*, *Araneus sturmi* (Hahn) on stand *F*.

On the basis of the index of constancy of species living in the pine trees 4 variants of the communities can be distinguished (Fig. 7): *A - B, C, D, E - (E), F, G - H*. Community *E* has certain features of the communities in the older plantations *A, B, C*, and certain features making it similar to the communities of younger stands (*F, G*).

As will be seen from the above, the index of similarity of constancy in species of web spiders, both in field layer and in pine trees, makes it possible to distinguish the same variants of communities which are correlated with the age of the forest stands.

### Abundance

The abundance of constant species in field layer fluctuates between 90–98% of the total numbers of spiders caught on each stand (Tab. VIII). The numbers of constant species in the pine trees, in comparison with the numbers of all species of each stand, is from 75 to 93% (Tab. VIII). The overwhelming majority of individuals caught thus belong to species occurring on all the areas. Taking the above figures as a basis it may be assumed that the same association of web spiders occurs on all the stands in each of the layers examined.

However, contrary to the specific composition and percentage of common species, the abundance of web spiders, both totalled and for each species, exhibits considerable differentiation on the stands examined (Tab. IV and V). It may be said in general that the same association of small web spiders occurs on these stands, but that the level of abundance is different; each community exhibits different productivity.

If the total numbers of spiders in the field-layer on stand *A* (the oldest pine trees) is taken as 100%, then in the next plantation in order of age (*B*) their numbers form 61%, and in the remainder 38%, 30%, 29%, 25%, 21%, 20%. Differences in the abundance of spiders between stands *A, B, C* (older) are statistically significant, and are not statistically significant between younger stands: of course the differences between older and younger stands are even more statistically significant. These differences are probably connected with the amount of food, which increases as the pine wood develops; the older stages create more ecological niches, and therefore contain more species – potential victims, which settle in these niches, supplying a larger amount of food for unspecialised predators, such as spiders are in general. This will be discussed more fully in the discussion of the results of this study.

The total absolute numbers of spiders on all the stands are determined by



the number of common species, and chiefly by the dominating and influent species (Tab. IV).

The numbers of the dominant, *M. acalypha*, and influent species, *D. arundinacea*, differ enormously on each stand (Tab. IV); for the first species, in uniform, comparable series of samples, numbers are from 130 to 640 individuals, for the second species from 4 to 236 (Tab. IV). *M. acalypha* is most numerous on stand A, which differs from the other stands by reason of the greater age of the pines and greater density of the plantation. Spiders in this environment (the richest both quantitatively and qualitatively in spiders) were caught on small open spaces surrounded by a dense forest stand. *D. arundinacea* also occurs there in large numbers, as it does on stand B.

Both dominating species occur in far smaller numbers on stands situated in the immediate neighbourhood of dunes (stands G, E, F). Abundance of *M. acalypha* there is only from 20–23%, and *D. arundinacea* from 1.6 – 9% of its greatest abundance (Fig. 8).

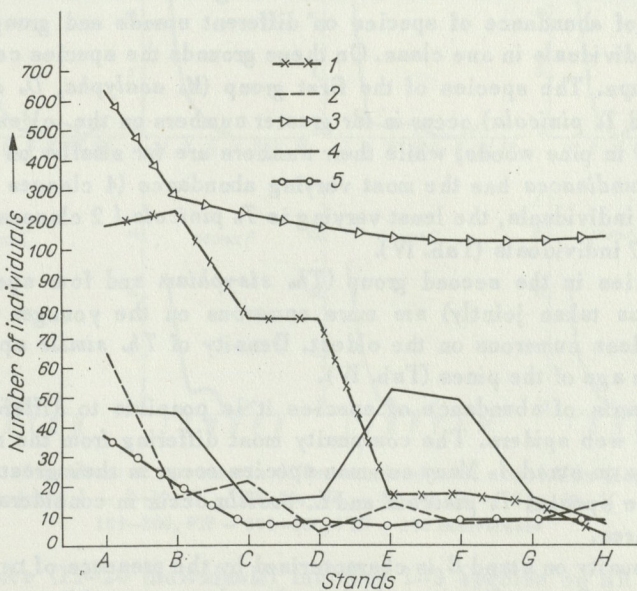


Fig. 8. Abundance of the most numerous species of web spiders in the field layer on each stand in 1959

1 - *Dictyna arundinacea*, 2 - *Linyphia pusilla*, 3 - *Mangora acalypha*, 4 - *Theridion simile*, 5 - *Tetragnatha pinicola*

*T. pinicola* is most abundant also on stands A and B, and on others forms only 19–20% of its numbers on stand A. *L. pusilla* is numerous only on stand A, on the remainder it forms from 8–34% of its greatest numbers. *Th. simile* occurs



in large numbers in the group of older pine plantations (stand *A* and *B*) and medium age plantations (*E* and *F*) on which it is three times as numerous as on the remainder (Fig. 8). *Th. sisyphium* is abundant on the stands situated near the dunes (stands *G*, *E*, *H*) (Tab. IV).

As can be seen from the above, the dominating, or influent species and certain more numerous of the common species, occur either all in very large numbers, or all less numerously on the same stands; on areas with younger pines the heather is more poorly settled than on the areas with older pines, although the younger stands are drier and sunnier (they grow on the habitat *Pineto-Vaccinietum myrtilli cladonietosum*) and the majority of the species (especially those in greatest abundance) are xerothermic forms. The probable causes of this phenomenon will be discussed in the discussion of this study.

The numbers of individuals in the common species occurring on different stands can thus be arranged in several classes of abundance, distinguished for each species separately; they are far more numerous on some stands than on others. Classes of abundance were formed, making use of the distinct differences in the level of abundance of species on different stands and grouping similar numbers of individuals in one class. On these grounds the species can be divided into two groups. The species of the first group (*M. acalypha*, *D. arundinacea*, *L. pusilla* and *T. pinicola*) occur in far greater numbers on the oldest or the two oldest stands in pine woods, while their numbers are far smaller on the younger stands; *D. arundinacea* has the most varying abundance (4 classes of numbers) from 236 to 4 individuals, the least varying is *T. pinicola* (2 classes of numbers) — from 7 to 37 individuals (Tab. IV).

The species in the second group (*Th. sisyphium* and four species of the genus *Araneus* taken jointly) are more numerous on the younger and medium stands, and less numerous on the oldest. Density of *Th. simile* appears not to depend on the age of the pines (Tab. IV).

On the basis of abundance of species it is possible to differentiate each community of web spiders. The community most differing from the remainder is the community on stand *A*. Many common species occur in their greatest numbers here. Of these species *T. pinicola* and *L. pusilla* occur in considerable numbers only on this area.

The community on stand *B* is characterised by the presence of two dominants: *M. acalypha* and *D. arundinacea*, which in the other communities examined is at most an influent or a species represented in very small numbers. This character, and also the far smaller numbers of *M. acalypha* and *L. triangularis* (from the community of medium-sized web spiders) distinguish it from the community on stand *A*, to which it is the most similar. Features in common are: great abundance of *D. arundinacea*, numbers greater than on the remaining stands of *T. pinicola*, considerable abundance of *Th. simile*, similar number of species.

The communities of stands *D* and *C* are similar, the community of stand *C* is however, richer both as to species and numbers, and is distinguished by



a greater abundance of *L. pusilla* and *Araneus adiantus* (this species belongs to medium-size web spiders).

The communities on stands situated between dunes are very similar, both as to number of species and their abundance. Area *H* is characterised by the occurrence of *D. arundinacea* in its smallest numbers (4 specimens) and *Th. simile* (7 specimens). Of the remaining three stands near dunes the community of stand *G* is the most clearly distinct. The total abundance of spiders and of *Th. simile* are far smaller here than on stands *E* and *F*. The communities of stands *E* and *F*, which are situated close to each other are, practically speaking, uniform as regards the numbers of each species and total abundance.

The greatest number of species comes within class I of abundance (Fig. 9), which groups together species which are not numerous (1–10 individuals), class

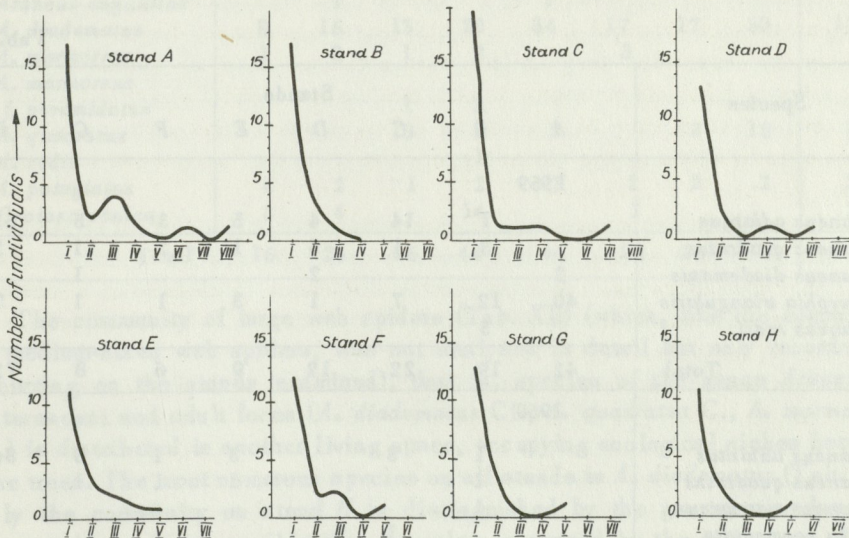


Fig. 9. Curves of numbers of species in different classes of abundance (data from 1959)  
Classes of abundance I – 1–10, II – 11–20, III – 21–50, IV – 51–100, V – 101–150, VI – 151–200, VII – 201–300, VIII – 300 individuals

II of abundance (11–20 individuals) includes 1–3 species on all the stands, class III (21–50 individuals) contains a different number of species – on certain stands there are no species in this class or only 1–2 species occur, while on stand *A* as many as 4 species occur in this class of abundance. Classes IV, V and VI (51–100, 101–150, 151–200 individuals) are empty or contain only one species. Classes VI and VII of abundance do not occur on some stands. A characteristic feature of these diagrams is the absence of one of the intermediate classes of abundance and the rise in the curve with the last class, which contains the predominant species. Features of this kind of the curve were considered and analysed by Gause (1936a, 1936b), Lityński (1938) and Williams (1944).



In the community of small web spiders in the pine trees, the differences in the total abundance of web spiders and of each dominating and influent species can be seen, as they can in the case of the heather but these differences are far smaller than in field layer (Tab. V). *M. acalypha* is a distinct dominant only on stand A, and even so shares domination with the species *Th. varians*. On stand F the most numerous species are *M. acalypha* and *Th. simile*. On other stands, in addition to the above mentioned species, the following occur in larger numbers — *A. cucurbitinus* and *Th. sisyphium* and on stand B — *D. arundinacea*; of all the common species 3–4 occur on each area in fairly large numbers, the differences in numbers between them being slight.

Abundance of medium sized web spiders  
in the field layer during the period from August to September

Tab. XI

Species	Stands							
	A	B	C	D	E	F	G	H
1959								
<i>Araneus adiantus</i>		1	14	4	5	3	5	65
<i>Araneus quadratus</i>		3	1	5	1	2	1	2
<i>Araneus diadematus</i>	2			2			1	
<i>Linyphia triangularis</i>	40	12	7	1	3	1	1	5
<i>Araneus redii</i>		3						
Total	42	19	22	12	9	6	8	72
1960								
<i>Araneus adiantus</i>		1	3		3	1	3	86
<i>Araneus quadratus</i>		1			1	1	1	
<i>Araneus marmoreus</i>		1						
<i>Meta segmentata</i>			1					
<i>Linyphia triangularis</i>	42	11	2	2	2		7	2
Total	42	14	6	2	6	2	11	88

Of the medium-sized web spiders (Tab. XI) *L. triangularis* occurs, like the majority of small web spiders, in its greatest numbers on stand A, while *A. adiantus* (only adult individuals of this species occur during this period) was not caught at all on stand A and was encountered in greatest abundance on stand H (65 individuals), which is distinguished by the smallest numbers of small web spiders. *A. adiantus* was caught in single individuals on all other stands except H. It would seem that the cause of the peculiar distribution of this species is to be found in the abiotic conditions of the hollow area (very sunny area of a mixed forest habitat *Pineto-Quercetum*, surrounded on three sides by dunes and thus to a large extent sheltered from the wind) forming on this stand a suitable climatic niche for both species of southern origin and xerothermic forms, rarely found



in Poland (presence of *Eresus niger* Petagna, *Phileus chrysops* Poda, *Thomisus onustus* Walck.). Dziabaszewski (1959) caught it both on damp meadows and on stands with xerothermic vegetation, and therefore it is not the humidity of the environment which determines its occurrence in large numbers, but most certainly exposure to sun and shelter from the wind.

## Communities of large argiopids

Tab. XII

Species	Stands								Total
	A	B	C	D	E	F	G	H	
<i>Araneus angulatus</i>		1			1				2
<i>A. diadematus</i>	8	16	13	20	34	17	17	50	175
<i>A. marmoreus</i>	1	2	1	2		3			9
<i>A. marmoreus</i> <i>f. pyramidatus</i>			1	3					4
<i>A. quadratus</i>			10	2	2		3	18	35
<i>A. redii</i>				1					1
<i>A. patagiatus</i>	4	2	1	2	7	2	2	2	22
<i>Cyclosa conica</i>	3	4		14		1			22
Total	16	25	26	44	44	23	22	70	270

The community of large web spiders (Tab. XII) (which, like the community of medium-sized web spiders, was not analysed in detail but only recorded as occurring on the stands examined), that is, species of the genus *Araneus* — maturescent and adult forms (*A. diadematus* Cl., *A. quadratus* C., *A. marmoreus* Cl.) is distributed in another living space, occupying ecological niches between pine trees. The most numerous species on all stands is *A. diadematus* (Tab. XII). Only the community on stand H is distinguished by the greater abundance of these spiders. It is possible that this also is caused by the situations of this stand, on which these spiders have especially suitable conditions for stretching their nets, since it is a dry, sunny and sheltered environment.

To sum up:

1. Differences in the abundance of spiders on the stands examined, both in field layer and in shrub layer, are large and statistically significant, both when taking into consideration the total numbers of the spiders and each of the more numerous species (Tab. IV, V, Fig. 8).

2. Differences in numbers are correlated with the age gradient of the pine trees, on the older stands the total number of spiders is greater than on the younger stands according to the age gradient of the pine trees; each species exhibits distinct differences in numbers on the stands examined; species of the greatest density *M. acalypha* and *D. arundinacea* also exhibit correlation with the age of the pines, if the stands examined are divided into groups of older and younger trees. Certain other species (less numerous than the common species) are more numerous on the younger stands (*T. sisypium* and species of the genus *Araneus*) (Tab. IV and V, Fig. 8).

3. The structure of abundance in the communities examined (Fig. 9), as was the case in examinations made by many other research workers (e.g. Gause) is as follows:



the majority of the species are represented by small numbers of individuals, certain classes of numbers are absent, species with great abundance of individuals form the minority (dominant species).

4. Of the medium-sized web spiders *L. triangularis* occurs in the greatest numbers on the stand occupied by the oldest pines, and *A. adiantus* on one of the youngest stands (the "hollow"). The greatest density of adult individuals of the genus *Araneus* is encountered in the "hollow", which may be connected with the ecological habitat requirements of the above species (Tab. XI, XII).

#### COMPARISON OF THE STRUCTURE OF A COMMUNITY OF SMALL WEB SPIDERS IN 1959 AND 1960

In order to discover which structural characters of the community of spiders are permanent and which vary from year to year, captures were made in the autumn of 1960 in the same way as they had been made in 1959 (5 series of captures consisting of 25 strokes of a sweep-net made 10 times during the August-September period), taking into consideration only the numbers of a few (five) frequently occurring species and the numbers of all small web spiders. Comparison of the numbers of spiders from both years leads to the following remarks.

1960 (very rainy and cool in both summer and autumn) is characterised by a smaller total abundance of spiders on the eight stands examined in the field layer of a pine wood. The spiders in 1960 form 49-86% of their numbers in 1959 on each stand (Tab. XIII, XIV). The cause of this phenomenon may

Abundance of small web spiders in the field layer during  
the period from August to September 1960

Tab. XIII

Species	Stands							
	A	B	C	D	E	F	G	H
<i>Mangora acalypha</i>	163	97	113	77	62	76	97	73
<i>Dictyna arundinacea</i>	84	188	116	118	20	59	34	7
<i>Linyphia pusilla</i>	173	41	47	9	34	17	16	19
<i>Theridion simile</i>	8	51	8	13	11	22	15	1
<i>Tetragnatha pinicola</i>	39	10	13	10	7	8	6	5
Others	102	48	39	23	23	33	30	34
Total	569	435	336	250	157	215	198	139

have been the delay (in relation to 1959) in the development of young spiders, their hatching from the eggs and migration into the heather of a large part of the spiders, caused by unfavourable weather conditions. When comparing the numbers of the three first series of captures such delay was in fact established. On the other hand the check of the numbers of spiders in the second half of September and the first half of October, made with the aim of determining whether differences in numbers arise only from the delay in the process of formation



Domination of most abundant common species  
in the field layer in 1960

Tab. XIV

Species	Stands							
	A	B	C	D	E	F	G	H
<i>Mangora acalypha</i>	29	22	34	31	39	35	49	53
<i>Dictyna arundinacea</i>	15	43	34	47	13	27	17	5
<i>Linyphia pusilla</i>	30	9	14	3.6	22	8	8	14
<i>Theridion simile</i>	1.4	12	2.4	5.2	7	19.2	7.6	0.72
<i>Tetragnatha pinicola</i>	7	2.3	4	4	4.5	3.7	3	3.6
Total percentage about	82	88	88	91	85	84	84	76
In comparison with 1959 the domination of <i>M. acalypha</i> was reduced by the following percentage	29	19	23	25	4	12	9	13

of the autumn community of spiders in the heather, or whether there are basis differences in numbers, such as the spiders exhibit in the two study years, showed the reality of this second phenomenon. No further increase in numbers of spiders in heather was found at the end of September. The general level of numbers is lower in 1960 (Fig. 10), which may be explained by the less favourable conditions for the xerothermic forms in the rainy and cool summer of 1960 in comparison with the dry and hot summer of 1959.

For purposes of comparison I have given the temperatures records (monthly means) and the monthly sums of rainfalls in July for these two years. July is the month of the greatest reduction of the young stages of web spiders. The majority of species examined hatched out from the cocoons at this date and dispersed over the vegetation.

	July	
	1959	1960
Temperature (monthly mean)	20.7	16.7
Rainfall (monthly sum)	129.7	199.8

Dice (1952) describes the phenomenon of variations in the abundance of spiders in the communities as a result of variations in the action of physical factors. A. Kajak (1960) also refers to the different levels in the numbers of meadow spiders in different years.

Comparison of total abundance and numbers of species on each stand shows



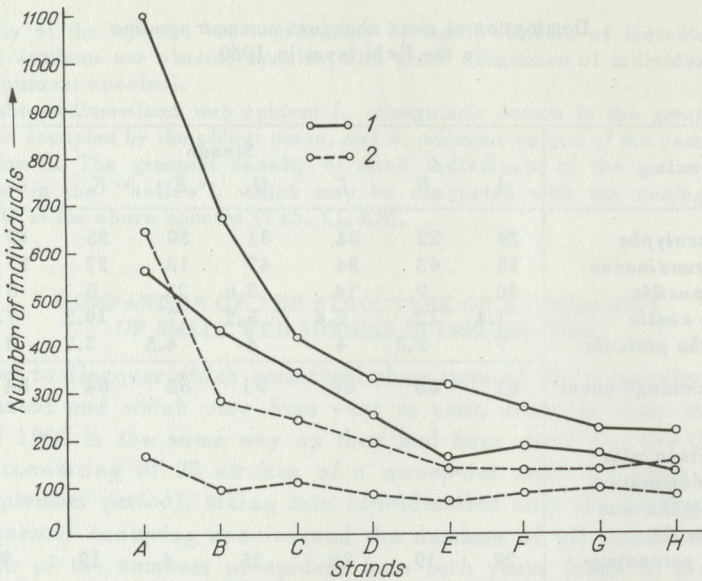


Fig. 10. Abundance of small web spiders in the field layer on each stand during the autumn period of 1959 and 1960

1 - all small web spiders, 2 - *Mangora acalypha*

that in 1960 also (Tab. XIII) stand A held the greatest number of spiders and, together with areas B and C (group of older stands) stands out reason of the level of abundance from the remaining group of younger stands. Differences in numbers between the older and younger stands are however, far smaller in 1960, since the greatest reduction of abundance occurred on the oldest stand (A) (Tab. XIV, Fig. 11). This shadiest and moistest (in comparison with other stands) stand did not in a rainy and cool year, even despite the large amount of food, constitute so suitable a place for xerothermic species as in a dry year with low rainfall.

*Macalypa* is reduced by 25%, *D. arundinacea* by 43%, *Th. simile* (xerobiont) by 17% and the euryhygric species, *L. pusilla*, increases by 266% (from 65 to 173 individuals).

The smallest reduction of abundance occurred on the youngest stand, one of the driest (Tab. XIV). *M. acalypha* occurred there in 73% of its numbers in the previous year, *Th. simile* in the same number of individuals, *D. arundinacea* in as much as 179% and *L. pusilla* in 200%. As can be seen, reduction took place only in the dominating species. The above variations in numbers clearly suggest that the chief factor which affected the fall in numbers consisted of weather factors; this agrees with the investigations made by Andrewartha and Birch (1954), who confirmed the views of certain ecologists (Bodenheimer 1938, Uvarov 1931, Dice 1952) distinguishing these factors as important in the variations in numbers of certain species.



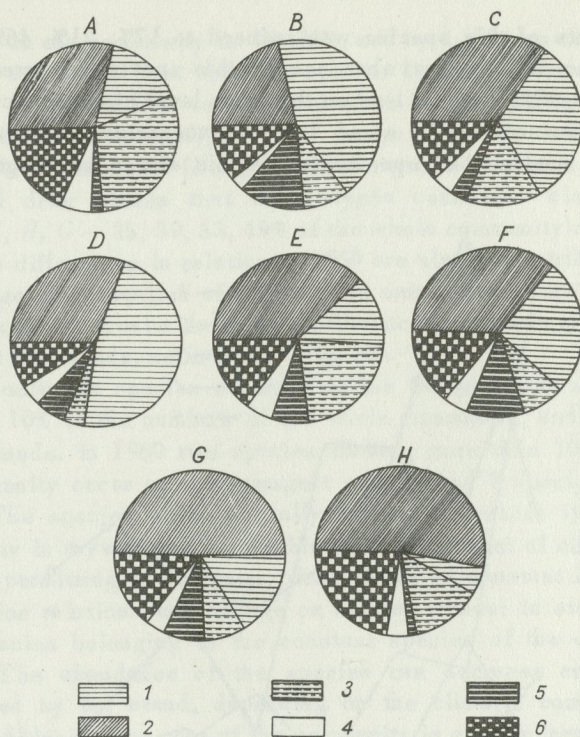


Fig. 11. Domination relations of small web spiders in the field layer in 1960

1 - *Dictyna arundinacea*, 2 - *Mangora acalypha*, 3 - *Linyphia pusilla*, 4 - *Tetragnatha pinicola*,  
5 - *Theridion simile*, 6 - other species

In 1960, therefore, the level of the abundance of each species underwent a change, but differences in numbers according to stand were on the whole maintained (Tab. XIII). The number of individuals of *M. acalypha* decreased considerably and its abundance on different stands became similar, exhibiting differences considerably smaller than in 1959 (Tab. XIII).

*D. arundinacea*, as in 1959, occurred most numerous on stand B. On stand A it underwent marked reduction (see above) while on stands D and C the level of numbers is the same, but higher than in 1959 (1959 - stands D and C: number of individuals 76, 76; 1960 - stands D and C: 116, 118); on stands G, E and F the level of numbers is the same, slightly higher than in 1959. In both years, on stand H, the individuals of this species occur only sporadically. *L. pusilla* increased the level of abundance from 100 to 150% on all stands (except stand H, where it occurs in the same number of individuals), maintaining differences in numbers on these same stands as in 1959. Therefore this species is most numerous on stand A, the oldest stand, less numerous on areas B, C, E; and very scanty on areas D, G, H.

The number of individuals of *Th. simile* decreased greatly on the whole: only on stand B was the same level of abundance maintained. On stands A, E



and *F* the numbers of this species was reduced to 17%, 21%, 46% of those in 1959. In both years the smallest abundance of this species occurred on stand *H*.

*T. pinicola* remains more or less on the same level of abundance as in 1959, and occurs most numerous on stand *A*. *Th. bimaculatum* is most numerous on stand *A*. The abundance of species in 1960 is shown on diagram (Fig. 12).

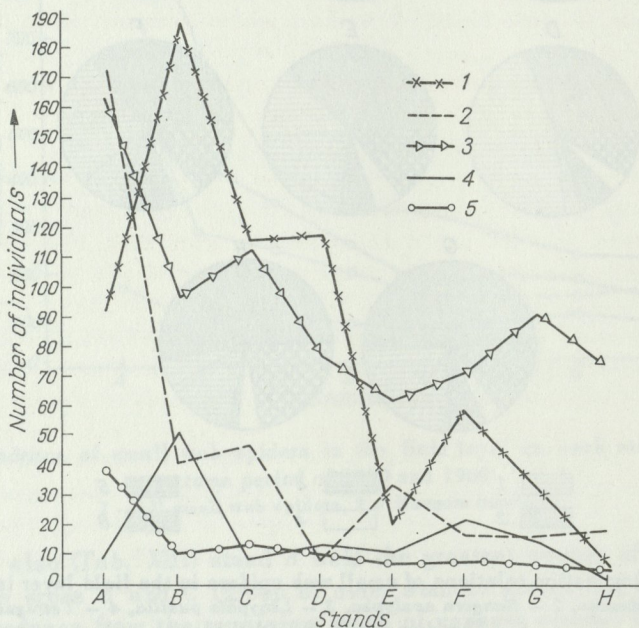


Fig. 12. Abundance of most numerous species of web spiders on each stand in 1960  
 1 - *Dictyna arundinacea*, 2 - *Linyphia pusilla*, 3 - *Mangora acalypha*, 4 - *Theridion simile*,  
 5 - *Tetragnatha pinicola*

The numerical relations and occurrence prevailing in 1959 among the medium-sized web spiders were maintained in 1960 also. *L. triangularis* occurs abundantly only on the two oldest stands, *A* and *B*. In 1959 the numbers of this species captured on stands *A* and *B* were respectively 40 and 12 individuals, in 1960 - 42 and 11 individuals in comparable series. *A. adiantus* occurs abundantly in both years on stand *H* only; captures in 1959 were 65, and in 1960, 86 individuals.

Domination relations underwent a far greater change in 1960 than differences in abundance relations on the stands examined (Tab. XIV, Fig. 11). It was impossible to distinguish dominants and influents in 1960 - there was no distinct transition between these types of species, an absence of the marked rise in numbers which existed in 1959 between the dominant and other species, and between the influent and accessory species.

*M. acalypha* is not an absolute dominant greatly exceeding the other species of the community in numbers. On the older stands *M. acalypha* reduces its



participation in the community by 19–29%, and by 4–13% on the younger stands. On stands *B* and *D* the most abundant species becomes *D. arundinacea* (43% and 47%) and *M. acalypha* falls to the level of an influent (22%, 31%); on stand *A* the equal partner of *M. acalypha* (29%) proves to be *L. pusilla* (30%), and on stand *C* – *D. arundinacea* (*Mangora* and *Dictyna* 34% each). It is only on the younger and drier stands that *M. acalypha* continues clearly to dominate (stands *F*, *E*, *H*, *G* – 35, 39, 53, 49% of the whole community). On these stands, however, the differences in relation to 1959 are also very striking – not only is the percentage of domination of *M. acalypha* smaller, but that of *L. pusilla* and *D. arundinacea* is greater (although differences in participation are evident depending on the stands, as in 1959) (Fig. 11).

In 1959 only one species occurred on the two youngest stands in numbers greater than 10% of the numbers of the whole community, and 2 species on the remaining stands. In 1960 two species forming more than 10% of the numbers of the community occur on the youngest stands, and 3 species on each of the remainder. The species which normally dominates reduces its participation in the community in a year less favourable to it on account of climatic conditions, in this way permitting of a greater participation of constant species (Fig. 11).

Domination relations can change on similar stands; in similar communities different species belonging to the constant species of the community can be dominants. The abundance of the species can decrease or increase within limits defined by the stand, depending on the climatic conditions prevailing (weather conditions). The core of the community is always formed from the same group of species which belong to species common to all similar stands, that is, to constant species of the communities, forming about 90% or more of the community and can take each other's places within certain limits.

#### COMPARISON FROM THE TIME AND SPACE ASPECTS OF COMMUNITIES OF SPIDERS

Comparison was made using material from the 5 most abundant constant species, the individuals of which form the great majority of all web spiders caught. Calculation was made of the index of similarity of domination and constancy for species in the communities on all the stands, comparing the communities of spiders in 1959 with those in 1960 (8 indices) and comparing with each other the communities on all stands in 1959 and all stands in 1960 (Tab. XV).

Analysis shows (Tab. XV) that the indices of similarity of the spider communities on the same stand are in many cases smaller from year to year than the mean of indices of similarity from different stands in the same year. This means that there is a series of cases in which the communities become less similar to themselves from year to year in the same place, than the 8 communities differing in space, investigated in the present work. Differences in the domination and frequency of species are in many cases greater within the same com-



## Indices of similarity

Tab. XV

Indices	Stands							
	A	B	C	D	E	F	G	H
Index of similarity of domination ( $Re$ )								
Mean $Re$ 1959	73	63	71	71	60	64	68	64
Mean $Re$ 1960	57	59	67	62	64	66	63	53
$Re$ 1959/1960	55	68	61	63	59	59	71	63
Index of similarity of constancy ( $Ku$ )								
Mean $Ku$ 1959	82	87	84	84	87	86	85	85.5
Mean $Ku$ 1960	78	82	84.5	83	83	87	86	80.5
$Ku$ 1959/1960	85.5	94.5	93	92	82.5	79	83	87.5

munity than between communities on different patches of vegetation. As it is extremely unlikely that the community occurring in the heather carpet in a pine wood changed from year to year into a different community, the facts described above are evidence that this same type of community (an association) occurs on all the stands examined

## DISCUSSION

The level of abundance of small web spiders depends to a large extent on the prevailing climatic conditions. In 1959, which was dry and warm, i.e. with very suitable conditions for the xerothermic forms, the level of abundance on all the study areas was higher than in the cool and rainy year of 1960. The general abundance is determined by the dominating and influent species, which in 1959 was generally *Mangora acalypha*, this being a species of spider loving light and dryness. It occurred in the greatest numbers on the oldest wettest and shadiest area.

In the generally dry and very hot year — differences in moisture and insolation in different dry environments were not great and did not affect the numbers of the spiders; in fact the reverse was the case: the environment which would seem to be the least suitable of all those investigated, was most densely settled. It may therefore be stated that microclimatic factors in the given conditions do not directly affect the abundance of the species, nor determine them: the causes of differences in abundance must be sought for elsewhere. Two hypotheses can be put forward to account for such considerable variations in numbers in similar environments.

The first of them, more general in nature, subordinates the abundance of an animal group to the stage of development of the whole biocenosis. It is a well-known fact from ecological research that with the development of succession the abundance of species and their numbers increases to the stage preceding the climax itself. This is connected with the formation of new ecological niches,



which are occupied by "new" species capable of forming food for the "old" species (that is, those already existing in the biocenosis of the previous stage).

Pillai (1922) states, that spiders in the older woods are represented in greater numbers than in the young plantations. Heydemann (1960) confirms that the number and abundance of species of spiders increased in the older stages of the succession which he investigated.

A young pine plantation about 16 or 17 years old already forms a different (to a certain degree) environment than an 8-12 year old plantation. Differences occur in the humidity and insolation which — may — although not must, as already found, always affect the abundance of spiders within the limits of variation occurring on dry areas — however affect the presence and abundance of their victims. In addition to abiotic differences, there are also biotic differences; the character of the young plantation alters, changing from a plantation of young small trees to a young pine wood, the volume of the pines increases thus permitting of the presence of more numerous species or increasing the possibility of distribution of the species already occurring on the young pine trees. All this contributes to an increase in the number and abundance of species which may be victims of the spiders, and by this means, to an increase in the number of spiders, since — as is well known from ecological literature — variations in the abundance of victims may affect the level of numbers of predators (Severcov 1941, 1951 and many others).

The second hypothesis is more detailed and is in fact a special case of the first; an increase in humidity and degree of shadiness of the environment affects the greater abundance of mosquitoes flying into the heather in the autumn (Dąbrowska-Prot 1960), which are the victims of small web spiders. A greater abundance of victims causes greater density of spiders, chiefly of the species *M. acalypha*, on the oldest area, while the lowest density is found on the youngest, dry stands (Tab. IV). Thus moisture and shade factors indirectly affect the abundance of spiders.

It is probable that in this case the abundance of spiders is the resultant of the action of both types of factors (through the increase in the number of ecological niches with the growth of the forest and through the influence of increased humidity and shade on the presence of mosquitoes).

In the spider communities occurring on the study areas it is noticeable that a certain group of species, to which the dominant forms belong, increases its abundance on the older areas. Both the hypotheses given above of course refer to this group. The second group of species, considerably fewer in number and not determining total abundance, occurs in its fewest numbers on the oldest area and more numerous on the medium and young areas; it is possible that biotic factors play a part here, e.g. interspecific competition; the problem requires further investigation.

A characteristic feature of the warm year 1959 is also the phenomenon of sharply-defined domination of one species. *M. acalypha* dominated on all the stands.



In the type of association investigated, the most numerous species in 1959 is not an ubiquitous species (such as, for instance, *Linyphia pusilla*) nor a specialised one, that is, adapted solely to one particular type of environment (such as *Theridion simile*), but a species with an ecological valence intermediate between them, for which the conditions prevailing in the environment investigated are more favourable, although it can also live in other habitats. Vestal (1914) described similar connections.

An interesting phenomenon is the complete change in domination relations and the participation in the community of each species during the rainy and cold autumn of 1960. It is difficult to distinguish a dominating species in that year on the basis of the accepted criterion (great difference in the abundance of the dominating species in comparison with others and lack of species in classes of abundance preceding the dominating species). In general 4–5 species participate to a fairly considerable extent in the community, differences in numbers not being as great as they were in 1959. In 1960 there was a great reduction in the numbers of the species *M. acalypha*, particularly in the oldest plantation. This suggests that the cool and rainy summer creates far less favourable conditions for this species than others. Although the conditions of the ecoclimate (moisture and insolation) may not affect the numbers of these spiders in a dry environment, in a warm and dry year, in a rainy and cool year they may exert a very strong reducing influence on the abundance of this species in environments less favourable to it. Reduction of the general level of abundance of *M. acalypha* on all the study areas in 1960 accompanies a rise in the level of abundance and participation in the community of other species, such as *Dictyna arundinacea*, *L. pusilla* and *Th. simile*. It would therefore seem probable that apart from the direct and indirect effects of abiotic factors, biotic factors also exert an influence: that of the reciprocal dependence between these species.

Spider communities therefore exhibit in 1959 a very similar structure of domination on all the areas despite the different level of abundance. This may mean either that 1) in 1959 the dominating species *M. acalypha* is here in its optimum environment, and other species are not – and that to a different degree, or that 2) competition between these species leads to the formation of similar structures in different places in the given type of environment, although the reduction in numbers is carried out by other factors, depending on the prevailing weather conditions.

The first supposition is based on the relation “species – environment” (abiotic conditions, food, structure and composition of vegetation), the second on the relation “species of spider – other species of spiders”. MacArthur (1960) divided the communities of animal species into two categories: into those, the numbers of which depend exclusively on the conditions prevailing in the environment (chiefly weather and food conditions) and alter adequately with the changes in these conditions, exhibiting considerable fluctuations in numbers and into a community in which balance is maintained, the numbers of which are relatively stable; the species of these communities are dependent on each other



in such a way that the rise in numbers of one causes a reduction in the numbers of a second. It would seem that it is not species of communities which belong to different categories, but that species of different communities exhibit under certain conditions a greater sensitivity to climatic influences (weather) and under other conditions, to interspecific connections. This is proved by the similarity of the domination structure in 1959 and its differentiation in 1960. A knowledge of the autecology of spiders shows that for at least a few of the ten constant species of a spider community in a young pine plantation with heather ground vegetation (*M. acalypha*, *D. arundinacea*, *Ih. simile*, *Ih. sisyphium* – all species loving warmth and light), at least a few of the study areas in the field layer may constitute an optimum environment; despite this, although on certain areas these species increase or decrease their participation in the community, this takes place within limits not disturbing the general domination structure. The conclusion may be drawn from this that in 1959, a favourable year for xerothermic species, *M. acalypha* is a species which wins in competition with other species, even with such for which the conditions in the given environment are also optimal or nearly optimal. In 1960, a rainy and cold year, domination relations undergo a change and are different on each stand; on certain stands *D. arundinacea* becomes the most abundant, and on all of them the participation of the euryhygric species, *L. pusilla*, increases. Climatic conditions (properly speaking weather conditions) act on the change in the relations between constant species. In a year "favourable" for the given species, the spiders are affected more strongly by the interspecific relations (influence of other species of spiders), which determine the level of abundance and participation in the community, in an "unfavourable" year the effect of weather conditions is stronger.

Elton and Miller (1954) write as follows on this subject: "Interspecific competition is taken as one example to illustrate that the distribution of species within interspersed community groups is not to be explained only by the set features of the physical environment or vegetation interacting with set characteristics of the species. The interaction of animal populations amongst themselves introduces other features, of which fluctuations and temporary replacement of one species by another are especially important. We need to know not only how many different ecological niches may occur in a community, but within each of them how many species may be in dynamic balance and how this balance may change".

The relative abundance of spiders (and probably of many other invertebrates) is dependent both on the environment conditions (ecoclimate factors, vegetation mantle, food) and on the reciprocal dependence between the constant species in the community. Relations between species change depending on the prevailing conditions of the habitat in which they live. The abundance of species of spiders and their participation in the community are defined in certain cases more by environment factors, and in others more by the action of intra-group factors. In the first case the effect of interspecific relations is of less



significance than the direct effect of weather conditions, and in the second case there is no direct influence of weather and food, while the interspecific factors are of primary importance.

## RESULTS

1. Phytosociological analysis based on the plants in the field layer showed that despite the general great similarity of the study stands, which belong to one type of environment (young pine plantation with heather) – the plantations examined grow on three different habitats: *Pineto-Vaccinietum myrtilli*, *Pineto-Vaccinietum myrtilli cladonietosum*, *Pineto-Quercetum*.

2. On all eight stands – regardless of phytosociological and other differences – the same association of small web spiders occurs. It may be termed an abstract community in the heather carpet of young pine plantations, growing on dunes in the Warsaw district. The criterion of the existence of an abstract community is the presence on the stands examined of 10 species of spiders common to all of them (constant species in the community), the numbers of which form from 90–98% of the numbers of all species caught on each stand.

3. The association examined exhibits variation in the following structural features: specific composition (apart from common species), total abundance, abundance of each species, domination, frequency.

4. All the above mentioned structural features of defined communities exhibit correlation with the age of the small pine trees, when dividing the environment into two groups: the older and younger.

5. The closest correlation with the age of the pines is exhibited by the total abundance of spiders in the community. If the total numbers of spider individuals in the field layer on stand *A* (the oldest pines) in 1959 are taken as 100%, then in the next plantation in order of age (stand *B*) these numbers form 61%, and on the remainder, in order of age from older to younger, – 38%, 30%, 25%, 21%, 20%.

6. The least correlation with the age of the pine trees is exhibited by the phenomenon of domination. On the two oldest stands there are different domination relations. On stand *A* the only unquestionable dominant is one species (*M. acalypha*), while two species dominate on stand *B* (*M. acalypha* and *D. arundinacea*).

7. The older stands are both wetter and less sunny and yet the numbers of spiders on these areas are greater, despite the fact that the numbers are established by the most abundant species of spiders which belong to xerothermic and photophilous species. In view of the above the possibility of the direct effect of microclimatic conditions (greater humidity and insolation) on the variations in numbers of the spiders in the habitats studied must be rejected, but numbers may be connected with the biotic conditions, changing with the development of the pine wood, the index of which is the age of the pines (increase in the number of ecological niches, increase in the number of victims).



8. Species common to all the stands (constants) may be divided into two groups. The species of the first group, to which the species *M. acalypha* and *D. arundinacea*, and also *L. pusilla* and *T. pinicola* belong, occur in far greater numbers on the stand or the two stands with the oldest pines, while their numbers are far lower on the younger stands. Species of the second group (*Th. sisymphium*, *A. cucurbitinus*, *A. quadratus*, *A. redii*, *A. diadematus* – juvenile forms) are more numerous on the younger and medium stands, and less numerous on the oldest stand. *Th. simile* differs from them, in that its density does not seem to depend on the age of the pine trees on the stand.

9. The numerical structure (ratio of number of species to their abundance) is distributed according to the well-known curve of the logarithmic series (Williams 1944), except that here the classes of numbers situated directly before the class of numbers of the dominant, are absent.

10. The association of web spiders in the pine trees is similar to the spider community in the field layer; it differs by the numerous occurrence in the pine tree layer of species characteristic of the bush layer: *A. cucurbitinus* and *Th. varians*. The participation in the community of certain species common to both layers is also different.

11. The domination structure of the association of web spiders in the field layer differs distinctly in 1959 from that of an analogical association in the pine trees. In the first case one species dominates, in the second several species (4–5) participate to a medium extent in the community (12 to 23%), while the participation of the remainder is very small. Among these more numerous species are species also more abundant in the field layer: *M. acalypha*, *Th. simile*, *Th. sisymphium*.

12. The general structure of domination of species in the field layer (one species dominating in 1959, several more numerous in 1960) is very similar in the given year on all the stands, while clearly marked differences are evident in the participation of each species in the communities of different stands, on the basis of which it is possible to distinguish the most similar communities.

13. Domination relations underwent considerable change in 1960. In 1959 the sole dominant is *M. acalypha*. In 1960 on the older (and simultaneously wetter) stands, different dominating species appear (from the group of constant species of the community) or at least attain the level of domination of *M. acalypha*; on the younger (and simultaneously drier) stands *M. acalypha* maintains its predominance, although its participation in the community has decreased.

14. The level of total abundance of small web spiders is lowered in the cool and rainy year of 1960, in comparison with the dry and warm year of 1959, while differences in total numbers on each stand are maintained, although they are not so distinctly marked as in 1959.

15. The greatest differences in the numbers of the species *M. acalypha* between the autumn of 1959 and 1960 were found on the oldest stand (A). In 1960 the numbers of this species were reduced by 29% in comparison with the autumn of 1959.



16. Comparison of indices of similarity of domination and constancy in the spider communities occurring from year to year in the same places and occurring in the given year on several of the patches examined is evidence of the fact that the same type of community exists there.

17. The hypothesis was put forward that the increase in the numbers of spiders in the older pine plantations is connected with an increase in the number of ecological niches occupied by the victims of spiders in the older stages of succession of the pine wood.

18. The hypothesis was put forward that the species in the community constituting a biocenotic unit, are under certain conditions more subject to the effects of weather conditions and in others – to interspecific influences (other species in the community), which is expressed in the variations in relative numbers of the species in the community. The structure of domination in a given community alters according to which factors play a bigger part in a given year.

The similarity of domination structure in a community of web spiders on similar stands in 1959 (a favourable year for xerophilous spiders) is evidence of the greater influence of interspecific relations in the community; differences in this structure in 1960 is evidence of the influence, greater than in 1959, of unfavourable weather conditions.

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RÓŻNICE STRUKTURY  
ZGRUPOWANIA PAJĄKÓW SIECIOWYCH  
JEDNEGO TYPU ŚRODOWISKA (MŁODY LAS SOSNOWY)

Streszczenie

Celem pracy było porównanie zgrupowań pajaków sieciowych żyjących w jednolitym zbiorowisku roślinnym, sprawdzenie czy tworzą one jeden typ zgrupowania, analiza różnic występujących między nimi oraz czynników, które to zróżnicowanie powodują. Obiektem badań były należące do jednej formy życiowej pająki sieciowe rozmieszczające się na wrzosie i na sosenkach młodników sosnowych na skraju Puszczy Kampinoskiej w okolicach Dziekanowa Leśnego. Połowy pajaków przeprowadzano w latach 1959 i 1960 metodą czerpaka (800 prób; jedną próbę stanowił materiał z 25 uderzeń czerpaka) i otrząsania w parasol entomologiczny (80 serii prób; jedną serię stanowił materiał z otrząsania 40 sosenek). Złowiono ogółem 7790 pajaków należących do 39 gatunków. Materiał zbierano w okresie względnej stabilizacji ilościowej i strukturalnej pajaków sieciowych (sierpień i wrzesień). Umożliwiło to łączenie materiału poszczególnych prób do analizy. Wybór obiektu badań (pająki sieciowe) i środowiska – uboższego i jednolitego, podyktowany został trudnościami metodycznymi. Czerpak, niemal jedyna metoda badań ilościowych pajaków sieciowych, daje stosunkowo najbardziej wiarogodne dane w środowiskach homogennych.



Sposób opracowania materiału polegał na wszechstronnym porównaniu zgrupowań pajaków z ośmiu powierzchni młodnika sosnowego różniących się głównie wiekiem sosenek (6 do 16 lat). Badano na nich skład gatunkowy, liczebność, dominację i frekwencję pajaków. Do porównania danych posłużono się wskaźnikami fitosocjologicznymi: podobieństwa gatunkowego (*QS*) Sørensen, podobieństwa dominacji (*Re*) Renkonena i podobieństwa stałości gatunków (*Ku*) Kulczyńskiego, układając je metodą Czekanowskiego i Kulczyńskiego. Badając stosunek liczby gatunków do wielkości powierzchni połowu ("species-area" method) stwierdzono, że pod względem liczby gatunków i stosunków ilościowych między gatunkami, badane powierzchnie zostały poznane rzeczywiście dokładnie.

Analiza materiału pozwoliła stwierdzić:

1. Pajaki sieciowe runa na wszystkich powierzchniach stanowią jedno zgrupowanie; to samo dotyczy zasiedlenia sosenek.
  - a. Olbrzymia większość (90–98%) osobników pajaków na każdym stanowisku należy do gatunków wspólnych dla wszystkich powierzchni (gatunki stałe zgrupowania). Są to gatunki wyznaczające liczebność wszystkich zgrupowań.
  - b. Różnice występujące w zgrupowaniach z roku na rok (1959 i 1960) na tej samej powierzchni są częstokroć większe do różnic występujących w obrębie zgrupowań różnych powierzchni w jednym roku.
2. Konkretnie zgrupowania pajaków sieciowych (runa czy sosenek) różnią się między sobą liczbą gatunków, składem gatunkowym, liczebnością, frekwencją i stosunkami dominacji.
  - a. Różnice liczebności, frekwencji i dominacji są skorelowane z wiekiem sosenek (najsłabiej dominacji); gęstsze zasiedlenie mają powierzchnie leśne starsze.
  - b. Pod względem liczby gatunków można zgrupowania ośmiu powierzchni podzielić na dwie grupy: zgrupowania powierzchni starszych (liczba gatunków: 26, 24, 23) oraz powierzchni młodszych (17, 18, 18, 17, 14).
3. Struktura zgrupowania pajaków runa jest różna w obu badanych latach.
  - a. Poziom liczebności ogólnej pajaków jest na wszystkich powierzchniach w 1959 roku, na skutek warunków meteorologicznych, znacznie wyższy niż w 1960, natomiast różnice liczebności między poszczególnymi stanowiskami (powierzchniami) utrzymują się w obu badanych latach w podobnych granicach.
  - b. Ogólna liczebność pajaków oraz liczebność poszczególnych gatunków jest na badanych powierzchniach w tym samym roku bardziej zróżnicowana niż stosunki dominacji, które w obrębie tego samego roku (zwłaszcza w 1959) układają się podobnie we wszystkich zgrupowaniach.
  - c. Stosunki dominacji ulegają w 1960 roku dużej zmianie w porównaniu z rokiem 1959. W roku 1959 jedynym dominantem na runie jest *Mangora acalypha*, w 1960 na powierzchniach starszych pojawiają się w większych ilościach inne gatunki (z grupy gatunków stałych) lub nawet dochodzą do poziomu dominacji *M. acalypha*; na powierzchniach młodszych *M. acalypha* utrzymuje znaczną przewagę, chociaż jej udział w zgrupowaniu zmniejsza się.

Na podstawie powyższych danych można stwierdzić, że zgrupowania występujące na ośmiu badanych powierzchniach stanowią pewien typ, którego trzonem są gatunki stałe; poza tym występuje grupa gatunków wymiennych, mało liczebnych i nie stanowiących ważnego z punktu widzenia ekonomiki biocenozy elementu zgrupowania. Gatunki stałe zgrupowania mogą zmieniać swoją liczebność i zastępować się w dominacji. Można przypuszczać, że wyższy poziom liczebności pajaków w starszych zagajnikach sosnowych wiąże się ze zwiększeniem liczby niszy ekologicznych, zajmowanych przez ofiary pajaków w starszych stadiach sukcesji lasu sosnowego.

Postawiono hipotezę, że gatunki zgrupowania, stanowiące jednostkę biocenotyczną są w pewnych warunkach bardziej podatne na wpływy warunków meteorologicznych, a w innych – na wpływy międzygatunkowe (innych gatunków zgrupowania), co znajduje



wyraz w zmianach liczebności względnej gatunków zgrupowania. W zależności od tego, jakie czynniki grają większą rolę w danym roku, zmienia się struktura dominacji określonego zgrupowania. Podobieństwo struktury dominacji zgrupowania pajaków sieciowych na podobnych stanowiskach w 1959 roku (korzystnym dla pajaków kserofilnych), świadczy o większym wpływie stosunków międzygatunkowych w zgrupowaniu; różnice tej struktury w 1960 roku świadczą o większym niż w 1959 roku wpływie niekorzystnych warunków zewnętrznych na formy kserofilne.

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