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ECOLOGICAL ANALYSIS OF TWO INVERTEBRATE GROUPS IN THE WET ALDER WOOD AND MEADOW ECOTONE

(Ekol. Pol. 21: 753–812). The phytosociological and microclimatic distinctness of the wet alder wood and meadow ecotone from these habitats is shown as well as the different structure and seasonal dynamics of mosquito and spider communities of the transitory zone.

Ecotone mosquito and spider species, which are as a rule the eurytopes, are distinguished.

The ecotone is defined as the zone of intensive penetration of mosquitos — potential prey of spiders — where as compared with the forest and meadow their possibilities to be caught by the predator are greater.

The ecotone is also the refuge zone for the invertebrate species in danger of intra- and interspecies competition.

Ecological compensation has been observed between two spider species inhabiting a similar ecological niche.

This subject was dealt with according to classical literature.

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1. INTRODUCTION

1.1. Definition of an ecotone and the aim of presented research

The contact zone of different biocenoses called the transition zone or ecotone (edge, Kontaktzone, Übergangszone) has been a matter of great interest for ecologists, both from the theoretical and practical point of view.

The differentiation of such an obvious landscape component as vegetational cover into separate vegetation types (formations, plant communities, etc.), and the existence of some kind of borders between them, were being observed for a long time. The observations were mainly concerned with the sharpness of these borders and the floristic distinctness of plant communities in the ecotone from those covering great areas, and with their dependence on the biotopic conditions.

The distinctness of the animal world in the ecotone of different biocenoses was also discovered many years ago. At first, the specific quality of this type of habitat and biocenosis there was examined in comparison to the neighbouring ones. Then, treating the ecotone as an important element of habitat mosaic, the mechanisms responsible for the formation of ecotone biocenoses were searched for.

However, there are very few papers dealing only with the studies of the typical for the ecotone animal communities and ecological phenomena. The material available is therefore composed of some facts and a thorough approach

to the subject is lacking. This is why we have taken such an interest in the subject.

The basic element for the invertebrates in the habitat is the vegetation forming a typical layer structure and the microclimate there. Therefore, in order to analyse two invertebrate groups – mosquitos and spiders – in the ecotone, a detail analysis of vegetation has been made both from the point of the differentiation of its floristic composition and structure and the formation of a specific life habitat for invertebrates. Also, to obtain clear results a very distinct ecotone has been chosen.

The ecotone studies have not only a theoretical value, but also a practical one. According to Odum (1959), the role of ecotone constantly increases due to the intensifying process of human economical activities resulting in continuous disintegration of habitats and biocenoses into smaller parts.

1.2. The ecotone in phyto- and zooecological literature

The problem of ecotone and its significance had to be faced both by authors writing about the substance and structure of plant communities and by those dealing with their classification and processes of plant succession. The same applied to those who tried to present cartographically the vegetation units, and all elaborating research methods in plant ecology.

No wonder then, that at the beginning of our century great personalities in geobotany, representants and founders of various phytosociological and ecological schools, expressed their views on the subject. Among others, before the II World War the following wrote on the subject: J. Braun-Blanquet, A. K. Cajander, F. E. Clements, G. E. Du Rietz, H. A. Gleason, V. Kujala, H. Kylin, J. Paczoski, L. G. Ramienskij, R. Scharfetter, V. N. Sukačev, A. G. Tansley, W. Wangerin, J. E. Weaver and others. The vast literature on this subject centred around the following aspects:

1. The borders between plant communities: whether they are sharp or continuous, that is whether there is a narrower or broader transitory zone between the types of vegetation.

2. The mingling of components of neighbouring plant communities: whether the elements of the community diffuse singly in the mass of the other, or, whether they are found on the contact zone of different communities in patches or islands.

3. The distinctness of the transition zone: whether the transitory zone is only a mixture of components of neighbouring communities, or has its own floristic features.

4. The connection between the changes taking place in the vegetation of the transition zone and the changes in the habitat: which of them is sharper – the vegetation or the habitat border – and whether the vegetation is susceptible to all changes in the habitat, or to some of them only.

However, this discussion was rather academic as there were almost no special studies on this subject. The views of particular authors, usually expressed in works of a more general nature (textbooks, monographs, research methods' manuals), depended mainly on their general methodological assumptions, and these, in turn, on the personal geobotanical experience of the person in question. Thus, even the most outstanding, earlier authors, for instance, Scandinavian scientists surrounded by poor, monotonous vegetation of the North, quite frequently expressed one-sided opinions ("the borders of vegetation types are always sharp" or "these borders are always broad, transitions are gradual"). Still, other geobotanists, working on areas with more differentiated natural conditions, observed a great variety in nature, and thus, the multiformity of the borders of vegetational cover types. The opinions of Paczoski (1925, p. 78) remain valid up to to-day. Already then, Paczoski understood that the transitions between particular plant communities may be gradual ones and from broad belts where the elements of neighbouring associations mingle together, and also, that they may be sharp, and rapid, but then the transition is narrow. He also knew that the sharpness of the border line depends on the floristic abundance of neighbouring communities and the extent of floristic affinity, and also on the sharpness of the gradient of the changes in the habitat.

Among the first, detail papers, consciously dealing exclusively with the problem of the transition zone, there is the paper by Nicenko (1948), who examined the border zone between the high peat bog and the poor coniferous forest. He made many charts and carried out also observations on transects. He noticed the small fluctuation of phytocenose borders in different years. The specific, insular character of the border and transition zone in these studies has been acknowledged as a common phenomenon.

A further progress from the methodical point of view and some more facts are found in the post-war Polish papers. Krankowska-Sznajder (1952) used in forest associations of the Białowieża Forest (E Poland) the method of belt transect (Clements 1905, Du Rietz 1921, Tansley 1923). Phytosociological surveys and soil examinations showed that the linear variation of vegetation and biotope are parallel and the width of transition zone depends on the extent of changes of the biotopic factors.

The most comprehensive from the methodical point of view is the work of Traczyk (1960). He uses also the method of belt transect from association

to association. The biomathematically elaborated floristic data from forest and peat bog associations, collected at Roztocze (SE Poland), are compared with the results of soil investigations. Therefore, the conclusions as regarding the width of the transition zone and its dependence on the quality of neighbouring plant associations and the changes taking place in the biotope fully confirm the already cited opinions of Paczowski (1925). Furthermore, Traczyk (1960) proves that only associations of a complex structure form transitions¹ of an insular character, as the high peat bog described by Nicenko (1948). He also confirms the observation made by Scharfetter (1932) that in the transition zone between two phytocenoses a narrow belt of floristically specific habitat may form, which by means of the two transition zones joins the large complexes of neighbouring associations. Traczyk (1960) points also to the dynamic character of the transition zones between plant associations in the succession stage.

Polakowska (1966) using the methods applied by Traczyk (1960) confirmed the majority of his conclusions on transition zones of other plant associations and in a different geographical region of Poland (Białowieża Forest).

Faliński (1962) submitted a proposition and proved that the borders of phytocenoses, and thus the ecotone range, change during the vegetation season. In belt transects between forest associations with distinct seasonal dynamics, he made phytosociological surveys twice (in spring and in late summer) on small squares. The situation of the borders of phytocenoses and the range of the ecotone between them were determined by three biomathematical methods including the entire species combination and it was found that the ecotone displays a seasonal variation in the range, and usually of the width also. Faliński determined also the regularities of the movement directions of the transition zone.

The studies on soil microflora point also to the difference of the relations in the ecotone biocenosis, from those in any one of the adjoining habitats. Kuźniar (1953) provided data on the soil microflora of the border line of arable field and pine forest. He showed that both the part of the field and the forest adjoining the border line have a smaller total number of microorganisms and lower biological activity of different physiological groups than in the open field and far in the forest. As the effect of the contact line decreases with the distance, the range of the effect of forest on arable soils may be determined using microbiological methods.

Quite a considerable contribution to the knowledge of the ecotone vegetation were the studies for practical purposes such as game management. Thus Barick (1950) studied the ecotone vegetation of numerous forest and

woodless associations in Adirondack in the States to explain the well known fact that the transition zones between plant associations create the best living conditions for the game. Barick carried also studies on the breadth of the ecotone and the floristic composition of its vegetation. He applied in his studies a modification of the belt transect with a different size of test areas for trees, shrubs and herb plants' vegetation and presented a detail graphic and mathematical analysis. These studies proved the existence of different ecotones, similarly as the later works of Traczyk (1960).

The numerous attempts, mainly on the part of agriculturists and foresters, to determine the essence and the range of the effect of forest neighbourhood on the ecological conditions and crops on adjoining fields, and the research on the effect of shelter belts on arable fields all over the world, greatly helped to understand the living conditions in the ecotone.

After the II World War, in Poland these studies centred mainly in southern Wielkopolska, in the area with a great variety of shelter-belts as far as their shape, size and age are concerned. The research of Kutera (1956), Wilusz (1956, 1958), Jaworski (1960, 1962), Jakuszewski (1967), Kamiński (1967), Wójcik (1973) and others show that in the direct vicinity of the forest, that is in the ecotone, the water relations in soil and microclimatic conditions are completely different than in greater distances from it, and the yield and structure of the crop of crop plants is different there. The practical aspect of this type of investigations is obvious, and on some areas with plenty ecotones these studies are of the utmost economical significance.

Numerous descriptions of plant communities from many countries brought a great deal of data about the vegetation. But the data were grouped according to various systems and thus needed systematizing. What's more the very foundations of the classification needed revision.

In the discussions between those who advocated the concept of separate plant associations and those who defended the idea of continuity of the vegetation, the problem of transition zone arose once more (Goodall 1963). The typological classification of plant communities, worked out by French-Swiss school of phytosociology (Braun-Blanquet 1951, Poore 1955), leaves out many transitional, hard to classify, communities between typical associations. If we accept a continuously changing plant cover (Whittaker 1956, Kalela 1960 and others), it becomes impossible to differentiate units and to classify anything, because every plot of vegetation is transitional. But notwithstanding the theoretical and methodical dispute about the validity of the method, it is obvious that man's activity brings about increasing differences between particular biocenoses thus creating a mosaic of ecologic

systems more and more differentiated and having more and more distinct limits (Kostrowicki 1972). The transition zones become more and more numerous.

The problem of ecotone in zoology appeared at the beginning of the century. In 1917, Cameron, when studying the insects of the meadow, pasture and mixed deciduous forest, observed the differences in the entomofauna of these biotopes and that the border zones between these biotopes were more intensively inhabited by some insect species from both biotopes. This was the zone where the entomofauna species of both associations mixed together.

Later on, the observations of Cameron (1917) were confirmed. For example, it was frequently found that the number of species and the population density of some of them in the ecotone differ much from the adjoining biocenoses: they are more or less numerous in this biotope. This is true for several groups of invertebrates, e.g., spiders (Dąbrowska-Prot and Łuczak 1968a, Peck and Whitcomb 1970), mosquitos (Dąbrowska-Prot 1961, Dąbrowska-Prot and Łuczak 1968a, b), ants (Dluski 1965), beetles and *Apterygota* (Cameron 1917), and vertebrates – e.g., birds (Beecher 1942, Johnston 1947, Barick 1950, Johnston and Odum 1956) or mammals (Barick 1950).

The preference of ecotones by animals may in some conditions have a considerable range. And so, Johnston and Odum (1956) found that about 30–40% of birds nesting on the examined area (Georgia, U.S.A.) were the ecotone species. Similarly Michalska (1970), examining the mining insects of Suwałki region (north-eastern Poland), found 8 *Lepidoptera* species and 4 *Diptera* species occurring exclusively in the ecotones of forest and open area.

Johnston (1947), in her studies of the ecotone of the forest and open area in Illinois, found it to be inhabited by a completely specific avifauna not found in any other biotype of forest or open area.

However, it should be taken into consideration that the ecotone is formed by the two neighbouring biotopes, and it is certainly not without significance what kinds of biotopes form the ecotone. This can be proved by the studies of Barick (1950), who found that the roe-deer and wood grouse changed their spatial distribution only in some types of ecotone, whereas in others their spatial distribution did not change.

The population of typical biotopes and of their ecotones by various animal species is not a static one and is subject to annual and seasonal changes. E.g., it was found that in autumn some mosquito and spider species move from the ecotone into the adjoining biotopes or disappear faster in the ecotone (Dąbrowska-Prot and Łuczak 1968a). The roe-deer and wood grouse

preferred the ecotones in spring as compared to other seasons of the year, and the differences in the intensity of populating the centre of the biotope and their ecotones changed in particular years (Barick 1950).

Some studies show that animals more strongly related to the ecotone than to other biotopes are the eurytopic species or at least those, which display a broad ecological tolerance. This has been observed both among vertebrates (birds – Wasilewski 1961) and invertebrates (mosquitos – Dąbrowska-Prot 1962, spiders – Dąbrowska-Prot and Łuczak 1968a). This is probably connected with the great variability of abiotic factors in the transition zone, which requires considerable adaptation abilities in animals populating this zone.

It seems that the specific biotopic-biotic system in the ecotone provides favourable conditions for predators, which readily use this biotope as a place for obtaining food. Dluski (1965) showed that some ant species (e.g. *Formica exsecta*) frequently wander to the ecotone far away from their nests and feed intensively there. Similarly the predators of moist forest biotopes the *Tetragnatha montana* spiders readily inhabit the ecotones, where mosquitos are about 70% of their prey (Dąbrowska-Prot and Łuczak 1968b). It is possible that the greater activity of mosquitos in the ecotone than in the adjoining biotopes, thus making it easier to catch them in spider webs, lures this species there. The predatory species of the litter, beetles from the *Carabidae* family, also wander to the ecotone in pursuit of food (Grüm 1971). It has been also found that the frogs are the most numerous in ecotone biotopes, where they mainly hunt for phytophagous insects, and to a lesser extent for predatory and saprophagous forms (Zimka, in press). Zimka assumes that this is due to the fact that the phytophagous insects in the ecotone are more active than the predators and saprophagous. And also, that the frogs by removing more animals from the phytophagous level than from the predator one may produce some changes in the biocenotic structure of the ecotone.

Elton and Miller (1954) point out that the biocenotic exchange between biotopes takes place by means of ecotones and therefore they are so significant in many ecological processes and phenomena, e.g., migration, meeting of individuals of populations of various species and so on. This is also confirmed by the cited papers on predation in the ecotone. Beecher (1942) is of an opinion that the ecotone has a decisive significance as regarding the numbers and variety of fauna. He claims that the population density of the majority of birds, and probably also of other animals, is the function of the number of ecotones per surface unit. On the other hand, Johnston and Odum (1956) are of an opinion that one of the reasons for the evolution of some bird species is the constant transformation of the biotopes into fine mosaic

ones. They say that in the areas, where the large forest complexes become smaller, the birds move for good from the typical for them forest biotopes into the forest margins.

Thus, in the present state of our knowledge of the ecotone we are fully aware of the separateness of composition and structure of the vegetation in this biotope and of the possibility of the formation of specific fauna there, frequently richer and more numerous than in the adjoining biotopes. Still, we do not know the regularity with which a separate biocenosis of the ecotone is formed and the extent of its durability and relations with the biocenoses of the adjoining biotopes, which form the given ecotone.

2. CHARACTERISTICS OF THE VEGETATION AND THE BIOTOPE OF THE EXAMINED ECOSYSTEMS AND THEIR ECOTONE

2.1. Description of the investigated area

The area examined is in the central part of the Kampinos Forest, in the forest inspectorate Kampinos (Warszawa province, Poland). This is the border line of one of the large belts of sandy dunes of the Forest, overgrown with pine and mixed forests, and of a wide bog depression with wet alder woods and moist meadows (Kobendza and Kobendza 1945). A large, rather dense, complex of alder woods in this border zone with slightly undulated terrain is divided into tongues and isles entering into other plant associations. In this physico-geographical situation the vegetation is differentiated and there are many transition zones between various forest and forestless plant associations.

The area chosen for the investigations is in the border zone of wet alder wood and a slightly higher situated meadow, which as can be guessed from the remaining forest vegetation, has been covered once with oak wood or a mixed forest with a considerable share of oak.

The examined transition zone between the forest and the meadow is an artificial one, because, similarly as the majority of meadows in Poland, this one is of the anthropogenous origin and is a result of wood cutting.

This ecotone, as usually in such instances, is a very distinct one – a high, poorly branched forest wall borders directly with the low grass community. Therefore, this ecotone is not only the border of different associations but also of classes of associations, and even of plant formations – forests and grasslands. Furthermore, as shown by the studies of vegetation and soil, even if the forest would remain, the transition zone between the two forest associations: wet alder wood and much drier mixed forest would be more or less in the same place.

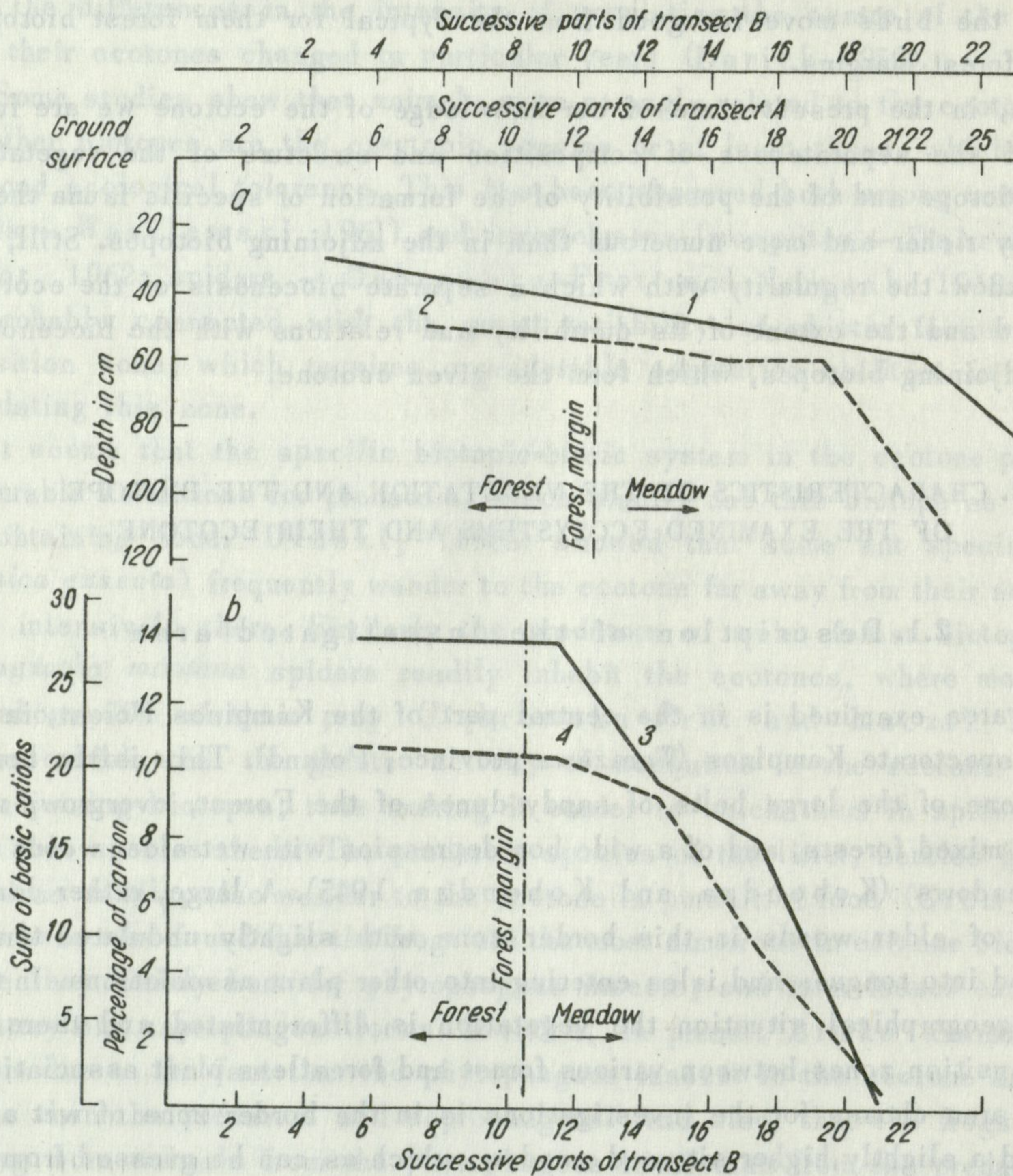


Fig. 1. a - ground water level in transect A and B. b - chosen chemical properties in transect B

1 - transect A (1970), 2 - transect B (1971), 3 - sum of basic cations (in milliliters - meg - per 100 g of soil), 4 - percentage of carbon

The soil studies show that the main factor responsible for the soil differentiation in the examined transition zone are the existing water conditions resulting from the different geomorphological history of the northern higher part of the area than its lower situated southern part.

In the depression under the wet alder wood there are gley "mursh" soils formed on sandy deposits with thin silty clay layers or a thin layer of silt loam at the bottom of the depression (alluvium of the Vistula proto-valley).

In the presence of water impervious layers the level of ground water does not drop below 50 cm. The conditions for the accumulation of organic matter are favourable and the easy oxygen supply during the considerable part of the year allows for rotting in its entire thickness. The colloidal complex, and mainly the organic one, is almost saturated with metal ions. The soil acidity is very low.

On the higher area, in the middle of the meadow, under the gramineous community of mat-grass (*Nardus stricta*) type there are poorly developed brown soil formed from loose, medium sand, most probably of eolithic origin. It frequently get too dry; the ground water level is usually below the depth of 50 cm. The conditions for the accumulation of organic matter are highly unfavourable. The colloidal complex is very small; the acidification process is distinct.

Apart from the soils of the depression and height we may distinguish soils of an intermediate character in the following order: gley "mursh" soils, murshy black earth, black earth, gley soils, and poorly developed brown soils.

The diagrams included point to the fall of ground water level towards the centre of the meadow (Fig. 1a) and the decrease in this direction of the organic matter content (per cent of °C) and the percentage base saturation of the colloidal complex (total exchangeable bases) (Fig. 1b).

2.2. Phytosociological characteristics

Within the several hectares of alder forest joined by the glade with a bigger and moister complex of such forest, a surface (80 × 60 m) quite uniform in its floristic composition has been chosen (Tab. I, surveys 1-9). The Table shows that the forest examined should be recognized as wet alder wood (*Carici elongatae-Alnetum* R. Tx. et Bodeau 1955). Only a narrow margin zone, moister and less forested differs slightly from the whole examined forest and therefore samples of mosquitos and spiders were not collected there.

From the point of floristic composition this forest is still a typical wet alder wood, but, due to the constant decrease of the ground water level in the Kampinos Forest, some changes have already taken place. At the moment the changes mainly observed in the vegetation composition are the quantitative ones and first of all the dominance of stinging nettles (*Urtica dioica*¹) in the forest floor. Furthermore, in the structure of the phytocenosis the disappearance of the typical for wet alder wood hummock structure is observed; the trees

¹Scientific names of plant species after Szafer, Kulczyński and Pawłowski (1967).

Plant communities of the alder wood

Tab. I

Successive number of the record	1	2	3	4	5	6	7	8	9	10	11	12	Constancy in records 1-9 1-12		
Cover of tree layer (%)	50	70	40	40	30	20	40	50	70	30	40				
Cover of shrub layer (%)	50	50	40	40	50	30	40	70		15	40				
Cover of herb layer (%)	60	70	50	50	60	70	70	50	40	90	70	60			
Cover of moss layer (%)		2	30	2								2			
Number of species	45	37	35	37	36	35	33	32	26	31	21	26			
Number of sporadic species	2			1						1	1				
Trees:															
<i>Alnus glutinosa</i>	3.2	4.2	3.3	3.2	3.2	2.2	3.2	3.2	4.2	2.2	3.2		V	V	
Ch. Carici elongatae - Alnetum:															
<i>Carex elongata</i>	1.2	+	1.2	1.2	1.2	1.2	1.2	1.2	1.2			1.2	V	V	
<i>Ribes nigrum</i>	2.2	2.2	2.2	3.3	2.2	1.2	2.3	2.3		1.3	1.1		V	V	
Ch. Alnetalia:															
<i>Dryopteris thelypteris</i>	2.2	3.2	3.2	2.2	1.2	2.2	1.2	1.2	1.2	1.2		+	V	V	
<i>Solanum dulcamara</i>	1.1	2.1	1.1	2.2	1.1	3.2	3.2	1.1	1.1	1.1		1.1	V	V	
<i>Lycopus europaeus</i>	3.2	1.1	1.1	1.1	2.2	1.1	1.1	1.1				1.1	V	IV	
<i>Salix cinerea</i>	2.2	2.2	2.2	2.2	2.2	1.2	2.2	2.1			1.1		V	IV	
<i>Calamagrostis lanceolata</i>	2.2	1.2				+	1.2	1.1		2.3		1.2	III	IV	
<i>Salix aurita</i>		1.1		1.2	1.1		1.1						III	III	
Accompanying species:															
<i>Filipendula ulmaria</i>	3.2	2.2	2.2	1.1	1.1	2.1	1.1	+	1.1	2.1	1.1	2.2	V	V	
<i>Poa trivialis</i>	2.2	3.3	2.2	2.2	2.2	1.3	1.3	3.3	2.3	1.3	2.3	3.3	V	V	
<i>Ranunculus repens</i>	2.2	2.2	2.2	3.2	2.2	1.3	1.2	1.2	2.2	2.2	2.2	2.2	V	V	
<i>Stachys palustris</i>	+	1.1	1.1	1.1	1.1	1.2	1.1	+	1.1	1.1	1.1	1.1	V	V	
<i>Galium aparine</i>	1.1	1.1	1.1	2.2	1.1	1.1	1.1	1.1	1.1	1.1	2.2		V	V	
<i>Iris pseudacorus</i>	1.1	1.1	1.1	1.1	1.1	+	+	1.2	1.1	1.2		1.1	V	V	

Plant communities of the ecotone

Tab. III

Number of record in table	1	2	3	4	5	6	7	8	9	10	11	12	Constancy
Cover of shrub layer (%)	5		15				40	5			5		
Cover of herb layer (%)	90	100	90	1000	100	70	80	100	90	80	95	100	
Cover of moss layer (%)	5			40		5	5		10	5			
Number of vascular plant species	32	20	20	26	17	23	29	20	20	22	24	19	
Number of sporadic species	4	2	1	2	1	3	4	1	2	3	4	4	
<i>Ch. Molinietales, Molinion and their associations</i>													
<i>Filipendula ulmaria</i>	1.1	2.2	1.1	2.1	2.1	2.2	1.1	2.3	3.3	3.3	3.1	3.1	V
<i>Deshampsia caespitosa</i>	2.2	2.2	3.2	4.2	3.2	2.2	1.2	3.2	3.2	2.2	2.2	2.2	V
<i>Geum rivale</i>	2.1	3.3	3.3	2.1	3.3	3.3	3.3	3.3	1.2	2.1	3.3	2.3	V
<i>Epilobium palustre</i>	+	1.1	1.1	1.1	1.1			1.1	1.1	+	1.1		V
<i>Festuca rubra</i>	3.2	2.2	1.2	3.2		1.2		2.3		+			V
<i>Lotus uliginosus</i>	1.1	1.1		1.1				+	1.1	1.1			III
<i>Valeriana officinalis</i>	1.3			1.1		+		+	+	+			III
<i>Lychnis flos-cuculi</i>	1.1		+	1.1					+	+			III
<i>Galium uliginosum</i>	+	1.1		1.2				1.1	3.2				III
<i>Cirsium palustre</i>	1.1					1.1			1.1	1.1	1.1		III
<i>Lysimachia vulgaris</i>						+	1.1			+	1.1		II
<i>Ranunculus auricomus</i>	1.1			2.1									I
<i>Stachys palustris</i>											1.1	1.1	I
<i>Stellaria palustris</i>							1.1			1.1			I
<i>Agrostis stolonifera</i>								1.2				2.2	I
<i>Ch. Molinio-Arrhenatheretea</i>													
<i>Rumex acetosa</i>	2.1	2.1	2.1	2.1	1.1	1.1		1.1	+	2.1	+	2.1	V
<i>Poa trivialis</i>	1.2	2.2		1.2	2.3	1.2	2.3		3.3	2.2	2.3	4.3	V

<i>Ranunculus acer</i>	3.1	2.1	1.1	2.1	1.1	1.1		1.1	1.1	1.1			IV
<i>Plantago lanceolata</i>	2.1	2.1	2.1	2.1	1.2				1.1				III
<i>Galium mollugo</i> (Ar.)	1.1	2.2	2.2	1.2	2.3			1.2					III
<i>Poa pratensis</i>	2.2	1.2	2.2	1.2	2.2								III
<i>Holcus lanatus</i>	2.2	1.2		2.2	1.2				1.2				III
<i>Cerastium vulgatum</i>			+					1.2			+		II
<i>Alectorolophus minor</i>		1.1							1.1				I
Accompanying species													
<i>Veronica chamaedrys</i>	1.1	2.3	1.2	1.2	2.1	1.1	1.3	2.2		2.1	1.2	1.1	V
<i>Galium palustre</i>	+			2.2	1.2	1.1	+	1.1	+	2.2	1.2	1.2	V
<i>Ranunculus repens</i>	1.1		1.2	1.1		1.2	2.1	1.2		2.2	2.3	2.2	IV
<i>Anthoxanthum odoratum</i>	2.2	1.2	1.2	2.2	1.2	1.2	+		+	1.2			IV
<i>Urtica dioica</i>					1.1	2.1	2.1	1.1			2.1	1.1	III
<i>Geranium robertianum</i>			+			+	2.3	1.1			1.1	1.1	III
<i>Calamagrostis lanceolata</i>						1.2	3.3		1.2		2.2	1.1	III
<i>Arabis arenosa</i>	+		+	+			1.1						II
<i>Galium verum</i>	1.1	+		1.1									II
<i>Chrysosplenium alternifolium</i>						1.1	1.1			1.1			II
<i>Galium aparine</i>						1.1	1.1						I
<i>Lysimachia numularia</i>						1.1	1.1						I
<i>Scutellaria galericulata</i>										2.1	1.1		I
<i>Potentilla anserina</i>	1.1			+2									I
Shrub and tree seedlings													
<i>Betula pubescens</i>	1.1		1.1				1.1	2.2			1.2		III
<i>Frangula alnus</i>	1.1		2.3				2.2				1.2		II
<i>Alnus glutinosa</i>							+				1.2		I
<i>Salix cinerea</i>							1.2				1.1		I
<i>Rhamnus cathartica</i>							1.1						I
<i>Padus avium</i>							1.1						I
<i>Quercus robur</i>							1.1						I
<i>Sorbus aucuparia</i>							1.1						I

no longer stand on "stilts" of their high roots, but their trunks grow straight out of the forest floor, and their surroundings are only slightly above the places without trees.

The meadow (Tab. II) adjoining the described forest is not such a floristically uniform biotope. It presents rather a mosaic of plant associations of a varying systematic classification. Close to the forest, in lower spots there are areas of periodically wet meadow of the *Molinietalia* order (Tab. II, records 1–5), on the whole poorly characterized. Further on in drier places, such communities contain also the species of the *Arrhenatheretalia* order (Tab. II, records 6–9). Then, in places are found areas of extremely poor biotope of fresh meadow (*Arrhenatheretum elatioris brizosum*) (Tab. II, records 10–15), developed especially well on large abandoned ant-hills. On the highest parts of the examined meadow there are smaller or greater areas of grass with a large share of mat-grass (*Nardus stricta*) (Tab. II, records 16–23) which are the transition stage from the mentioned sub-association of fresh meadow with quaking-grass (*Briza media*) in the direction of a drier community of the *Nardo-Callunetea* class. All these meadow communities, despite some differences, show a considerable floristic similarity.

The transition zone between the forest and the meadow is the narrow (1–30 m) zone of herbaceous vegetation with very few, scattered trees of birch (*Betula pubescens*) and black alder (*Alnus glutinosa*) and single shrubs or small shrubberies, mainly of alder buckthorn (*Frangula alnus*), sallow (*Salix caprea*) and young birche.

The breadth of this belt differs according to the local moisture conditions and mainly to the insolation time per day, which varies greatly on the indented forest margin.

These are (Tab. III) fragments of periodically wet herbage meadow belonging to *Filipendulo-Petasition* alliance (of the *Molinietalia coeruleae* order, *Molinio-Arrhenatheretea* class) typical of margins of alder woods (Nowiński 1967). Because of their fragmentary development it is difficult to classify them to a determined association.

An idea of mutual similarities and dissimilarities in the floristic composition of the examined plant associations is given by the diagrams of floristic similarity according to Czekanowski (Kulczyński 1939–1940). The coefficients of floristic similarity are calculated acc. to the formula of Sørensen (1948) (cf. Section 4.2), known in Polish botanical literature as the formula of Jaccard and Steinhaus. These diagrams (Fig. 2), have been elaborated on the basis of the phytosociological records of a surface 5 × 5 m, made in two belt transects cutting the examined area in the straight line from the forest interior to the open meadow. One of them goes across the ecotone

Plant communities of the meadow

Tab. II

Number of the record in table	1-9									10-15						16-23						Constancy in records					
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	1-5	6-9	10-15	16-23
Cover of vascular plant layer (%)	90	100	100	100	100	100	90	90	100	80	90	90	80	80	90	80	80	90	85	100	80	90	80				
Cover of moss layer (%)	40	20	30	40	20		10							5	10	10	5	5	10	5	5	5					
Number of vascular plant species	14	25	24	26	20	22	35	35	34	30	34	29	32	37	27	36	35	33	34	25	22	24	14				
Number of sporadic species	1		2	3	1	1	1	5	4	4	4	1	3	6		3	5		2		2						
<i>Deschampsia caespitosa</i>	2.2	2.2	2.2	4.2	2.2	2.2	2.2	4.2	3.2	2.2	2.2	3.2	1.2	1.2	3.2	2.2	3.2	3.2	1.2	2.2	3.2		5	5	V	V	
<i>Anthoxanthum odoratum</i>	2.2	2.2		2.2	1.2	2.2	2.2	2.2	2.2	2.2	2.2	2.2	2.2	3.3	3.2	1.2	2.2	2.2	+	2.2	2.2	2.2	4	4	V	V	
<i>Plantago lanceolata</i>	3.1	3.1	2.1	2.1	2.1	2.1	2.1	2.1	2.1	2.1	2.1	2.1	2.1	2.1	3.1	2.1	2.1	3.1				2.1	5	4	V	IV	
<i>Festuca rubra</i>		3.2	3.2	3.2	3.2	2.2	3.2	2.2	2.2			2.2	2.2	2.2	1.2	2.2	2.2	+	+	+	2.2	1.1	4	4	V	V	
<i>Rumex acetosa</i>	2.1	2.1	2.1	2.1	1.1	2.1	1.1	1.1	2.1	1.1	2.1	2.1	2.1	2.1	2.1		2.1	1.1	+	+	1.1		5	4	V	IV	
<i>Galium verum</i>	1.1	2.2	+			+	2.2	2.2	2.2	2.2	2.2	1.1	1.1	1.2	2.1	2.2	1.1	2.2	2.2	+		2.2	4	4	V	IV	
<i>Holcus lanatus</i>	2.2	3.2	1.2	2.2	2.2		3.2	1.2		3.2	1.2	2.2	2.2	3.2	1.2	3.2	3.2	1.2	3.2	1.2		2.2	5	2	V	IV	
<i>Ranunculus acer</i>	1.1	1.1	+	2.1		1.1	1.1	1.1		1.1		2.1	2.1	2.1	2.1	2.1	1.1	1.1		+	1.1	1.1	4	3	V	V	
<i>Euphrasia rostkoviana</i>		2.1	2.2		1.1	1.3	1.3	2.2	2.3	+	1.1				3.3	2.3	+	r	2.3			1.1	3	4	III	IV	
<i>Veronica chamaedrys</i>		2.1		1.2	2.3		1.1	2.2	2.2	+	1.1	2.1	2.1	2.1		1.2	+	1.1	1.2				3	2	IV	III	
<i>Arabis arenosa</i>		+		+		+	+	+	+		1.2	1.3	1.2	+	1.2	+		+	+		+		2	4	IV	III	
<i>Leontodon autumnalis</i>		1.1	+			2.1		1.1	2.1		+				2.1	2.1	2.1	1.1	2.1			1.1	2	3	II	V	
<i>Senecio jacobea</i>		+					+	1.1		1.1		+		+				+			+		1	2	III	II	
<i>Filipendula ulmaria</i>	1.1			2.1	1.1				1.1														3	1	.	.	
<i>Lotus uliginosus</i>	1.1	1.1		1.1	1.1		+	1.1	1.1	+		1.1											5	3	II	.	
<i>Geum rivale</i>	3.3	2.1	1.1	2.1	3.3		3.3	2.2	2.1			2.1	2.2										4	3	II	.	
<i>Potentilla anserina</i>	1.2		1.2	1.2		1.2						+			+								4	3	II	.	
<i>Lychnis flos-cuculi</i>	1.1			1.1			+	+		+		1.1	1.1	1.1									2	2	IV	.	
<i>Galium uliginosum</i>	2.1	1.1	1.1	1.2	1.1		1.1	1.1	2.1	2.1	1.1		+	+	1.1		1.1			+			5	3	IV	II	
<i>Poa pratensis s. str.</i>		1.2	1.2	1.2		2.2										1.2							3	1	.	I	
<i>Epilobium palustre</i>		+	1.1	1.1	2.1		1.1				+					+							4	1	I	I	
<i>Cirsium palustre</i>		1.1			+		+																2	1	.	.	
<i>Polygala vulgaris</i>		1.1	1.2				1.1	1.2			1.1	+	+	+	1.2								2	2	V	.	
<i>Mentha arvensis</i>		1.1	+		2.3	1.2			1.2						+			1.2	2.3				3	2	.	II	
<i>Linum catharticum</i>			2.2			2.3	2.2	1.1															1	3	.	.	
<i>Ranunculus repens</i>			1.2	1.2				1.2					1.3										2	1	I	.	
<i>Valeriana officinalis</i>			1.1	1.1			+	1.1	1.1			1.1	+	+									2	3	III	.	
<i>Trifolium repens</i>			1.2			+	1.2						+										1	2	I	.	
<i>Alectorolophus minor</i>			1.1			+		1.1		+	1.1		+	+	+	+	r	1.2			+		1	2	IV	IV	
<i>Ranunculus auricomus</i>				2.1								1.1		1.1									1	.	II	.	
<i>Potentilla reptans</i>				+			+	1.2	+								+						1	3	.	I	
<i>Equisetum arvense</i>				1.2						1.2	1.1		+	+			+						1	.	IV	I	
<i>Galium mollugo</i>				1.2	1.3	1.2	1.2	2.2	1.1	1.1	1.2		1.2	1.2	2.2	1.2	1.1	1.2	1.2	1.2	1.2	1.2	2	4	V	V	
<i>Potentilla erecta</i>					+		1.2	1.2	1.1	1.1	2.2		+	+	2.2	1.1	1.2	1.2	1.2				1	4	IV	IV	
<i>Festuca pratensis</i>						1.2	2.2	1.2	1.2	1.2	2.2			2.2	1.2	1.2	2.2	1.2	+			2.2	.	4	III	IV	
<i>Carex hirta</i>						1.2	1.2	1.2	1.2	1.1		1.1	+	+	+	1.2	1.2	1.2				1.2	.	4	IV	III	
<i>Agrostis vulgaris</i>					3.2			1.2		1.2	1.2			2.2	1.2	1.2	2.2	2.2	2.2	1.1	2.3	2.2	.	2	III	V	
<i>Companula patula</i>								1.1	1.1	1.1	1.2	1.1	+	+	1.1	1.1	1.1	1.1	1.1				.	2	V	III	
<i>Luzula campestris</i>							+	+			1.2	2.2	2.2	1.2	1.2	+	+	1.1		1.2		2.1	.	2	V	IV	
<i>Cynosurus cristatus</i>								+		1.2	1.2		+	1.2	+	1.2							.	1	IV	III	
<i>Linaria vulgaris</i>								+			1.1				1.1		1.2	+	+				.	1	I	III	
<i>Briza media</i>									1.2	1.1	1.2	1.1	3.2	2.2	2.1	1.1	1.1	1.1	2.2		2.2	3.2	1	1	V	IV	
<i>Avenastrum pubescens</i>										1.2	1.2	3.2	1.2	2.2	+		1.1				1.2		.	.	V	II	
<i>Achillea millefolium</i>										+	1.2	+			2.2	2.3	+	1.2	1.2	1.2	+	1.1	1.2	.	.	IV	V
<i>Hieracium pilosella</i>											+				+		1.2	1.2	1.2	2.3	1.2	4.3	.	.	III	V	
<i>Poa pratensis angustifolia</i>												1.2	2.2	1.2	1.2	1.2	2.2	2.2	+	1.2	2.2	1.2	.	.	IV	IV	
<i>Sieglingia decumbens</i>														+	2.3	1.2	1.2	1.2	1.2	+	1.1	1.2	.	.	II	V	
<i>Armeria elongata</i>														1.2		+	+	2.3	+	1.1		2.1	.	.	I	IV	
<i>Hypericum perforatum</i>															1.1	+	1.3						.	.	.	II	
<i>Nardus stricta</i>																1.3	1.2	3.3	3.2	5.2	4.2	+	.	.	.	I	V
<i>Viola canina ericetorum</i>															+					1.2		1.2	.	.	.	II	
<i>Veronica officinalis</i>																+		1.2	1.3	+			.	.	.	III	
<i>Rumex acetosella</i>																		1.2	1.1	1.1	1.1	2.3	2.1	.	.	.	IV
<i>Carex pallescens</i>																				+	1.2		.	.	.	II	
Shrub and tree seedlings																											
<i>Alnus glutinosa</i>	1.1							1.1				+											2	1	.	.	
<i>Frangula alnus</i>	+	+																					2	.	.	.	
<i>Betula pubescens</i>			1.1					1.1										1.1	+				1	1	.	II	
<i>Salix cinerea</i>										+													.	.	.	I	.
<i>Rhamnus cathartica</i>												++										+	.	.	.	I	I
<i>Quercus robur</i>													1.1									+	.	.	.	I	II
<i>Juniperus communis</i>																					+		I

Number of the record in table
Cover of vascular plant layer (%)
Cover of moss layer (%)
Number of vascular plant species
Number of spongy species

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	
2	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	
3	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	
4	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	
5	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	
6	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	
7	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	
8	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	
9	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	
10	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	
11	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	
12	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	
13	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	
14	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	
15	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	
16	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	
17	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	
18	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	
19	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	
20	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	
21	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	
22	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	
23	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	
24	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	
25	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	
26	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	
27	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	
28	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	
29	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	
30	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	

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Plant communities of the meadow

Tab. II

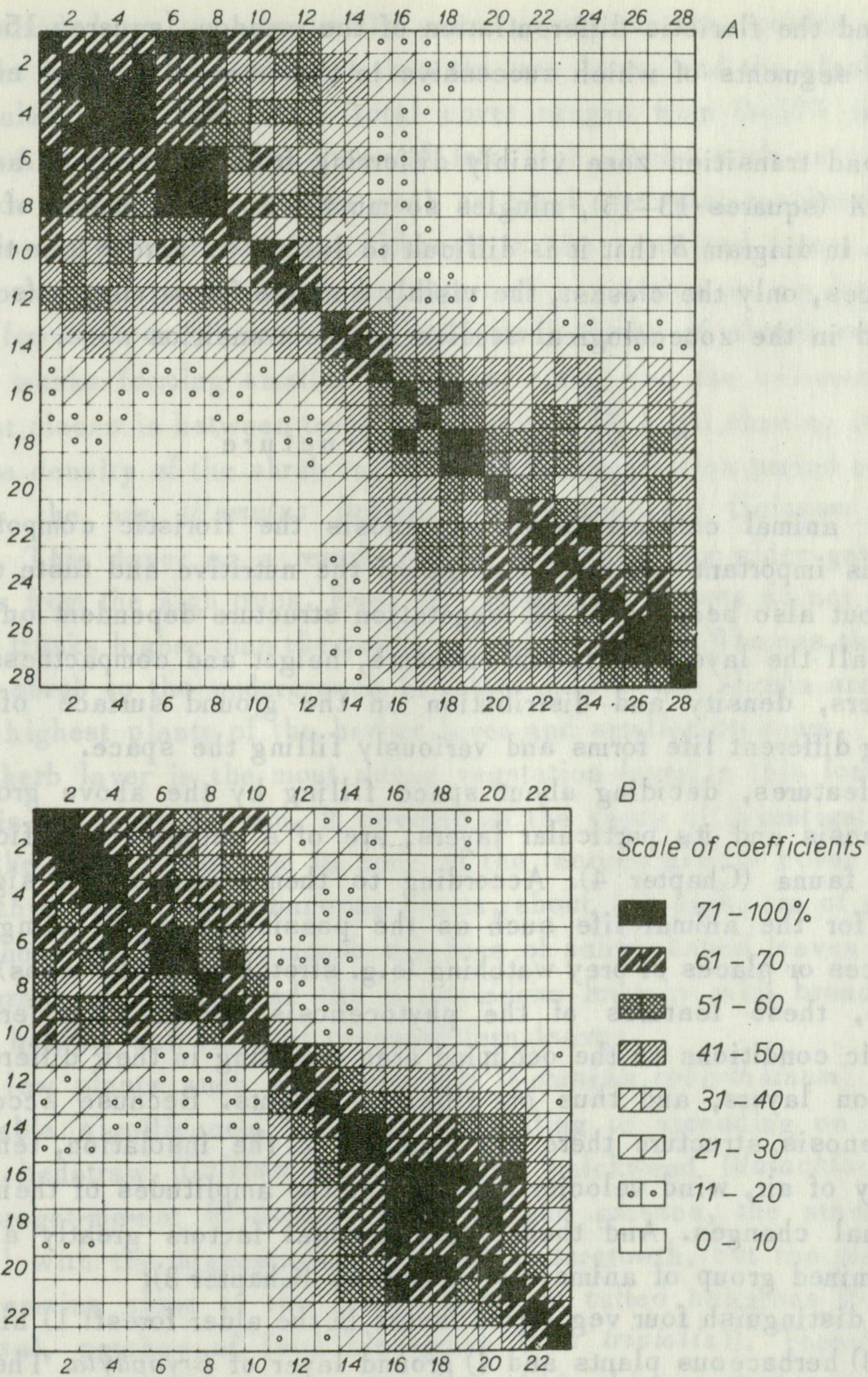


Fig. 2. Diagrams of floristic similarity of plant communities of alder wood, meadow and their transition zone (acc. to Czekanowski, after Kulczyński 1939-1940)

A - transect across the broadest transition zone, B - transect across the most narrow transition zone

herbage in the widest point (Fig. 2A) and the other in the narrowest one (Fig. 2B). On these diagrams, similarly as in the phytosociological tables, a great floristic uniformity of the wet alder wood is visible (squares 1-9

and 1–7) and the floristic differentiation of the meadow (squares 15–28, and 13–23), the segments of which successive in the transect form an ecological series.

The broad transition zone visibly differing from the meadow and forest in diagram *A* (squares 13–15), mingles so much with the complex of meadow communities in diagram *B* that it is difficult to delimit its border from this side. In such places, only the closest, the visibly herbage forest margin (square 11) was included in the zoecological studies as the transition zone.

2.3 Vegetation structure

For the animal components of biocenosis the floristic composition of vegetation is important not only because of the nutritive and taste qualities of plants, but also because of the vegetation structure dependent on it. This is first of all the layer vegetation structure, height and compactness of particular layers, density and distribution on the ground surface of species representing different life forms and variously filling the space.

These features, deciding about space filling by the above ground part of phytocenosis and its particular layers, are of a decisive significance for the spider fauna (Chapter 4). According to them, various and significant conditions for the animal life such as the possibilities of finding shelter, nesting places or places of prey watching (e.g. stretching spider webs) change. Furthermore, these features of the phytocenosis affect considerably the microclimatic conditions on the occupied area resulting in their differentiation in vegetation layers, and thus on different heights. Because according to the phytocenosis structure there are changes of the insolation, temperature and humidity of air, wind velocity and also of the amplitudes of their diurnal and seasonal changes. And these environmental factors greatly affect the second examined group of animals – mosquitos (Chapter 3):

We may distinguish four vegetation layers in the alder forest: 1) high trees, 2) shrubs, 3) herbaceous plants and 4) ground layer of *Bryophyta*. The crowns of high trees, specifically uniform, are not so uniform as regards compactness. The projective cover of crowns ranges in particular records from 30 to 70%. The regrowth alder mainly growing in groups leave a large part of the forest floor (several tens to 100 m²) uncovered by crowns. However, because these trees are high, these seemingly “open” areas are also a forest considerably shaded from all sides. The conditions in such places are typical forest ones as shown by the vegetation of the forest floor, which is almost identical under the tree crowns and in the gaps between them.

The shrub layer not always the same as regards the species composition and height is even less compact than the tree layer, and the shrubs are even less regularly distributed. Its total cover ranges from 0–50% in particular surveys. A division can be observed into high shrubs such as cherry, alder and willow and into low shrubs such as black currants, raspberries and the young growth of high shrubs. Although in the examined forest the typical for wet alder woods hummock structure of vegetation is no longer visible and the forest floor is more even, still the majority of shrubs centre around the tree trunks forming smaller or greater tufts, and the willows there take the lowest places in between trees and provide additional shading in the forest gaps. The density of the shrub layer during the vegetation period considerably increases the hop (*Humulus lupulus*) and bittersweet (*Solanum dulcamara*) creepers. This layer as a result of the lack of young alder growth visibly separates from the high trees. Even the highest hop shoots do not creep along the alder trunks higher than the peaks of highest shrubs. Whereas the transition from the shrub to the undergrowth is rather mild – low shrubs are not higher than the highest plants of the herbar layer and smaller creepers.

The herb layer is the most dense vegetation layer in this forest, and its density is the most uniform. It covered in the years of investigations almost 60% of the forest floor, and in none of the records did its cover come under 40%. In this layer, big herbaceous plants, about 1 m high, are of great importance. These are both the monocotyledons of sabre-shaped leaves (iris, large sedge, grass and rush) and the dicotyledons branchy with broad leaves on different heights and tufts of pinnated fern leaves.

The low plants such as cranes bill (*Geranium robertianum*) are also of considerable significance, as well as trailing or spreading on the ground, such as bedstraw (*Gallium aparine*) water chickweed (*Malachium aquaticum*), water forget-me-not (*Myosotis palustris*) and grasses, the stems of which are level with the highest plants of the undergrowth, but the main mass of leaves remains close to the ground [tufts of tufted hairgrass (*Deschampsia caespitosa*), patches of fowl blue-grass (*Poa trivialis*)]. Therefore, further division into two parts may be observed within this vegetation layer, but the proportion of the average cover of high plants to low plants is about 60%.

The ground moss layer is poorly developed in this forest and is broken into small tufts, strips and patches, mainly on the dead, rotten branches and trunks. And also a considerable part of the forest floor is not covered by vegetation.

The structure of plant communities on the examined meadow is much simpler, usually two-layer. The gramineous vegetation of the meadow covers everywhere the surface with a dense carpet (at least 90% of the cover),

but the height of the turf shows some differentiation. The lowest vegetation (with *Geum rivale*) is on some most moist areas in the forest vicinity and in the patches with *Nardus stricta* farthest from the forest as well as on the paths across the meadow. The typical meadow communities where high grasses prevail have the highest vegetation.

In full vegetation (from June, and even mid-May till August) the gramineous vegetation attains the height 50–80 cm and visibly divides into dense turf 15–30 cm high and the layer of grass hollow stems and floriferous shoots of dicotyledons 50–80 cm high, but not filling the space and rarely crossing it.

Furthermore, in damper places there is a ground moss layer, usually divided into smaller tufts forming bigger ones only in the lowest parts of the meadow (Tab. II, records 1–5) under the herbar layer. The moss tufts are also found in the driest parts dominated by the mat-grass. On a greater part of the meadow this layer is not found at all.

The vegetation structure in the transition zone between the forest and the meadow is similar to the structure of meadow communities as the vegetation of the examined ecotone is almost void of trees. The dicotyledons prevail and their occurrence is constant and dense. The vegetation of this herbage zone is higher than the average height of the meadow, and some stratification may be observed. The lower layer (20–30 cm) and dense (70–100% cover) consists of strongly developing dicotyledons, and first of all *Geum rivale*, *Lotus uliginosus*, *Ranunculus repens* and *Veronica chamaedrys* and out of grasses *Deschampsia caespitosa* and *Poa trivialis*. Higher layer (50–100 cm) is formed first of all by *Filipendula ulmaria*, and among the herbs there are *Urtica dioica*, *Valeriana officinalis*, *Cirsium palustre*, *Lysimachia vulgaris*, *Stachys palustris* and among grasses *Calamagrostis lanceolata*. This vegetation layer, although less dense than the previous one, fills the occupied space more thoroughly than the layer of grass blades on the meadow. The ground layer of mosses is only here and there in the ecotone, usually in small clumps.

2.4. Climatic conditions

2.4.1. General

For some animal groups, especially the moisture requiring mosquitos, the atmospheric conditions are of special significance. The composition and number of mosquitos are reflected both by the changes of macroclimate taking place from year to year and the microclimatic biotope differentiation depending

on the plant formation and thus the vegetation structure. Therefore, analyses of microclimatic differentiation of the examined area and macroclimate analyses are especially important because of the observed advancing drying of the examined area.

2.4.2. Macroclimate

During the four years (1966–1969) of ecological studies in the Kampinos Forest, also climatic observations were made in the basic meteorological station 3 km from the studied area. The data illustrate the course of minimal and maximal values of temperature and relative air humidity during the ecological studies, i.e., from mid-June till the end of October. Also, the temperature and relative humidity of air at 12 a.m. were also taken into account as this is the least favourable time of the day for mosquitos.

The diagrams of temperatures and relative humidity of air (Fig. 3) show a gradual decrease during these four years of minimal daily values and noon values of air humidity, and also a decrease in the two last years of the maximal daily relative humidity in summer months. The minimal and maximal daily and noon air temperatures also have a tendency to decrease in value, but less so.

The analysis of these data shows that during the four years of studies the climate in the Kampinos Forest was becoming gradually drier, and therefore the life conditions for the vegetation and moisture-requiring animals much worse.

Since 1968, both in the examined area and almost in the entire Kampinos Forest, drought symptoms were clearly visible and become more intense in 1969. The flavescence and falling of leaves from trees and shrubs began earlier that year than in the previous years. In the middle of August a large amount of leaves, especially of birch and willow, were found on the forest floor. Before the middle of September the autumn colours could be seen in all places where these trees grow among the pine woods, i.e. forest margins, clearings, besides the roads. 11 September 1968 the majority of leaves on birch, young oak and ash, on alder buckthorn, and different willow species, were yellow. The alder leaves falling when green were already strongly thinned away not only in the ecotone but also in the interior of the wet alder wood, where the soil even in the hollows was on the surface quite dry.

As found later, this drought affected also the pine needles. In September 1970 the needles in the third section from the end, i.e., those from 1968, turned russet and shed in great quantities. Therefore, the pine trees looked very much as the deciduous trees during the flavescence of leaves.

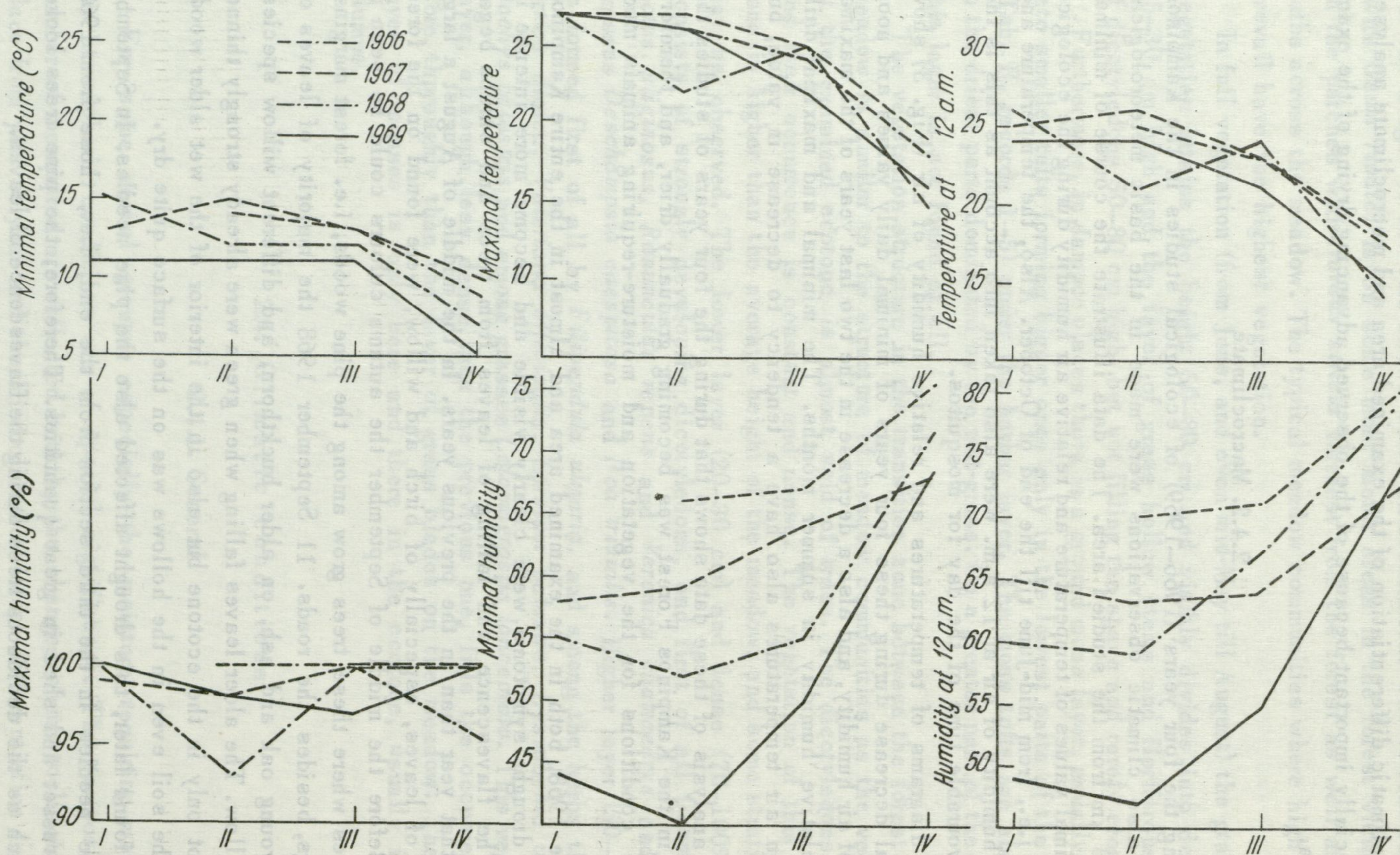


Fig. 3. Macroclimate of the examined area in 1969, 1968, 1967, 1966 periods: I – 17 VI–7 VII, II – 8 VII–9 VIII, III – 10 VIII–14 IX, IV – 15 IX–31 X

In the herbage of the transition zone, in August 1968, the large-leaved dicotyledons (*Filipendula ulmaria*, *Urtica dioica*) and leaves of more delicate grasses (mainly *Poa trivialis*) began to wither. In September, these plants dried up in the green state not only in the ecotone, but in places also under the forest roof. Thus the thinning of vegetation in the transition zone resulted in lower humidity in lower air strata and the transition zone was no longer the life habitat for mosquitos and other moisture-requiring animal species.

2.4.3. Microclimate

Microclimatic studies were conducted in all three biotopes – wet alder wood, mid-forest meadow and the transition zone between them. For 24 h. the recorders – thermographs and hygographs – were simultaneously placed in these three biotopes at: 1) cloudless sky and heat, 2) variable weather with occasional clouds and wind and 3) variable weather with a sunny morning and clouds and rain in the afternoon, night and early morning.

12 daily recordings of temperature and relative humidity were obtained. The daily course of changes in temperature and humidity in extreme atmospheric conditions are presented in Figure 4a, b. They show that at sunny and hot weather both the temperature and relative humidity on the meadow are considerably different than in the forest and ecotone. The latter are very much alike. On such days, the meadow as compared with the two other biotopes has a high temperature and very low air humidity. But at cloudy and rainy weather the temperature and relative air humidity is similar in all three biotopes.

As the differences between the temperature and relative air humidity on the meadow, in the forest and ecotone, are observed only during the day (at night these values are approximate to one another) therefore, the factor here is the direct insolation warming the meadow surface and thus warming and drying the air above it. Therefore, it is the factor differentiating the examined biotopes from the point of weather conditions.

All the resemblance of temperature and relative air humidity in the forest and ecotone is due to the fact that although the ecotone is overgrown almost by treeless vegetation it remains the greater part of the day in the shade of the forest, the margin of which is situated WSW-ENE and deviates from the W-E direction only by 20°. This shade is even greater thanks to the single trees and shrubs scattered in the transition zone and to irregular line of forest margin.

The observations made on the longest day of the year (24 June 1970, 3.14 a.m. – 8.01 p.m.) showed that the examined mid-forest meadow, in a cloudless weather, was insolated from about 4.40 a.m. to 7.30 p.m., i.e., almost 15 hours.

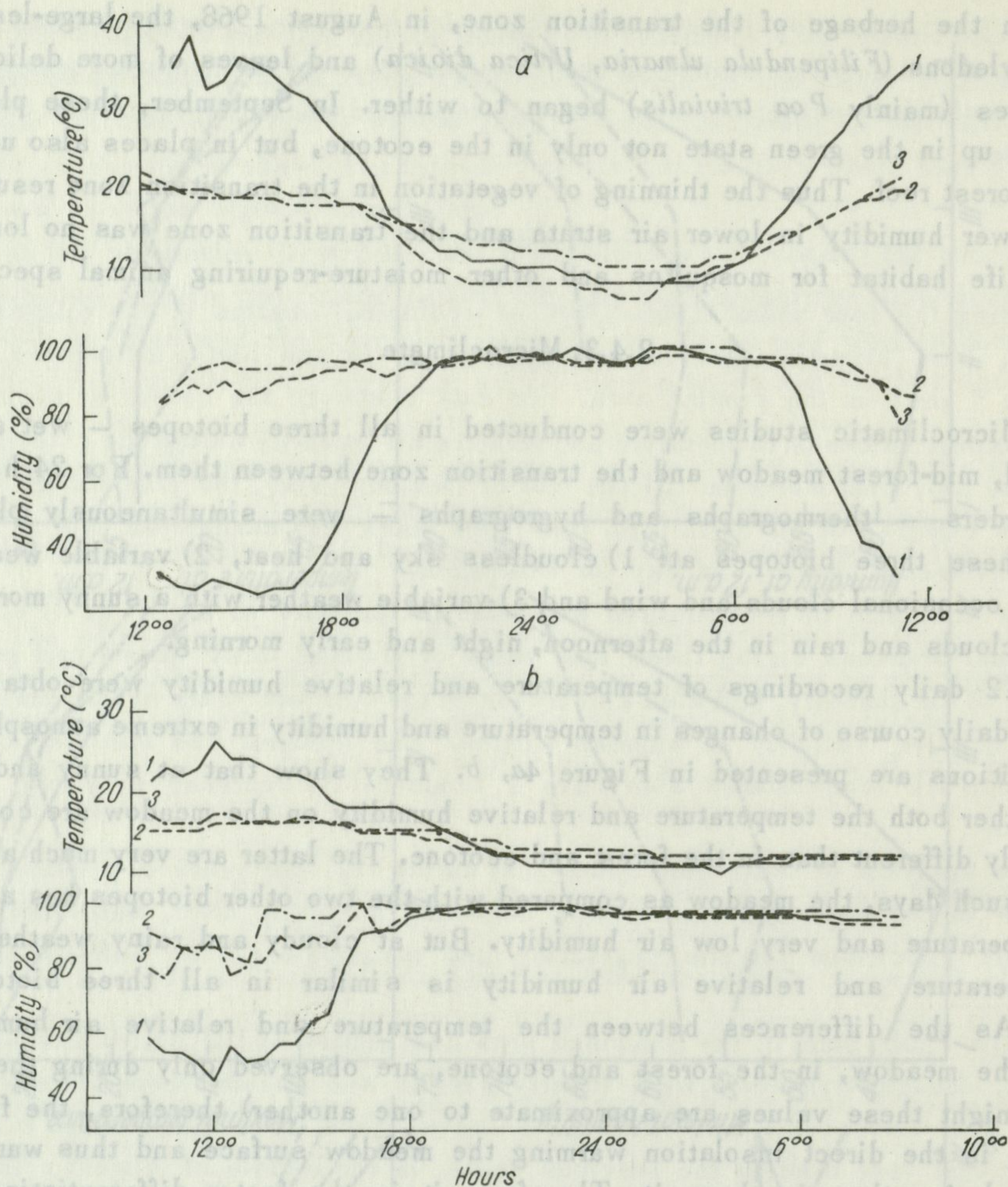


Fig. 4. Daily temperature and humidity course in the three examined biotopes: *a* — in conditions of hot weather, *b* — warm, sunny day, rainy at night, 1 — meadow, 2 — ecotone, 3 — alder wood

But in the ecotone, bright, insolated spots appear only in some places for an hour and then move into a different place, similarly as in the forest. In the morning, the shading extends over the largest area and its range delimitates the herbage vegetation (domination of large dicotyledons). The narrowest shaded belt is in the early afternoon, and then the greatest part of the herbage strip is in full light. The width of the shaded herbage zone, which varies on the 80 m examined section, depends on the height of trees forming the

forest margin in the given place. Thus it is the narrowest where the forest margin is formed by shrubs, and is the broadest beside high trees and in the recesses of the forest.

In the daily course of temperature and relative air humidity at different weather conditions we may distinguish four periods, varying as to their distinctness, in the three biotopes: 1) evening temperature decrease and humidity increase, 2) night stabilization of these values, 3) morning temperature increase and humidity decrease, 4) daily period of stabilization of values. The characteristic ones are the changes taking place in the evening and the morning.

Changes in temperature and humidity during the day (period I), at night (period II) and in the morning (period III) in the three examined biotopes, measured by standard deviation

Tab. IV

Weather		Fine weather, cloudy light wind			Fine weather in the morning, cloudy afternoon, and rain all night till the next day			Hot weather		
		period I	period II	period III	period I	period II	period III	period I	period II	period III
site	Humidity (%)									
meadow	22.8	0.7	42.5	25.1	1.5	0.9	49.4	1.7	41.3	
ecotone	24.4	1.0	21.9	5.1	0.8	0.5	4.2	1.2	4.0	
alder wood	5.3	0.9	11.5	9.5	0.7	0.4	6.7	1.7	7.0	
meadow	24.7	8.3	23.4	18.1	3.5	5.7	28.4	17.2	25.1	
ecotone	15.3	2.6	15.3	7.1	0.9	4.3	12.7	17.6	16.0	
alder wood	12.9	2.6	10.8	5.8	4.0	0	8.6	12.6	16.1	

The changes in daily temperature and relative humidity vary in different biotopes. These differences are not only visible in the daily temperature and humidity amplitudes, but also in the standard deviation from their mean value (Tab. IV). The minimal variability of temperature and humidity at night in all biotopes and in the majority of weather conditions is quite striking as well as the great variability of weather conditions in the evening and the

morning, furthermore on the meadow and their relative stability in the forest. Therefore, the ecotone is much more alike the forest than the meadow.

The characteristic feature of changes in temperature and humidity in the morning and the evening on the meadow is their high rate: e.g. from 5 p.m. to 9 p.m. (4 hours) the humidity increases from 38 to 95%, and the temperature decreases from 38 to 11°C, from 7 a.m. to 11 a.m. (4 hours) the humidity decreases from 95 to 28% and the temperature rises from 12 to 37°C. Therefore, the biotope, in a relatively short time, changes its value as the shelter for fauna, and especially for the humidity-requiring organisms as, e.g., mosquitos. Both in the forest and the ecotone such violent fluctuations in temperature were not observed, even when the weather favours the microclimatic differentiation of particular periods during the twenty-four hours (Tab. IV).

3. MOSQUITO COMMUNITIES OF THE WET ALDER WOOD, MEADOW AND THEIR ECOTONE

3.1. Methodics

Two methods of catching were used. Inactive mosquitos, sitting in the herb layer, were caught in the grass and shrubs with an entomological sweep-net; each time a series of 10 samples was taken (each series consisting of 25 strokes of the sweep-net). The active mosquitos, flying at the moment of sampling, were caught in 15 min. using as a bait a man sitting still.

The sizes of samples according to the previously obtained results as regards the minimal sample size were allowing for correct analysis of quantitative and qualitative changes taking place in the mosquito fauna (Dąbrowska-Prot 1966). This is especially significant because of the great differences in the mosquito abundance during the two years of investigations and requires such choice of the sample size as to be able to compare the material from both years.

The samples were taken twice a week from mid-June to mid-August, i.e., from the period of the maximal, summer number of mosquitos to the beginning in the second part of summer seasonal decrease of mosquito number. Thus the catches included both the period, in which the mosquitos were a significant biocenotic element because of their number and intensity of penetration of the examined area, and the period of the basic early-autumn changes in the number, structure and behaviour of mosquitos.

The characteristics of mosquito communities in 1967 and 1968

Tab. V

Catches	Abundance of mosquitoes (average)		Number of species		Uniformity of mosquito distribution (in standart deviation)		Per cent of <i>A. punctor</i> , <i>A. vexans</i> , <i>A. communis</i> in whole fauna			Structure of mosquito communities (Per cent of species)					
										1967			1968		
	1967	1968	1967	1968	1967	1968	1967	1968	1968	dom-inant	subdom-inant	accessory species	dom-inant	subdom-inant	accessory species
Sweep-net	49.5	10.29	6	4	94.5	141.5	6.1	13.3	76.5	12.4	11.1	82.9	10.9	6.2	
Bait	115.0	32.00	9	6	83.8	110.0	12.2	25.0	61.3	22.3	16.4	69.1	19.5	11.4	

3.2. The structure of mosquito communities

The mosquito communities on the examined area in 1967 and 1968 differed basically: the number of mosquitos, structure of the communities and their spatial distribution varied (Tab. V). As already mentioned, the climatic conditions were different in both these years, thus affecting mainly the level of mosquito abundance. In 1968, the mosquitos were much less numerous and were only about 27% of the mosquito fauna number in 1967. The difference regarded both the inactive mosquitos and the active ones. Also, in the second year of the studies the number of species decreased (Tab. V). In 1968, two species were not found: *Aedes flavescens* Müller and *A. excrucians* Walck; but the percentage of *A. punctor* Kirby, *A. vexans* Meig. and *A. communis* De Geer increased (the two first ones are known as species well surviving drought — Dąbrowska-Prot 1966). It should be mentioned that the examined area was rather poor as regarding the number of found mosquito species.

The changes in the structure of mosquito communities resulted in an increase in 1968 of the share of the quantitatively dominating species at the expense of the subdominant and accessory species (Tab. V). The unevenness of spatial distribution of mosquitos also increased. This is why the mosquitos in the second year

of studies aggregated in the most favourable biotopes for them in these weather conditions.

The species composition and the percentage of species in mosquito communities in both years are presented in Table VI.

Number of species and percentage of individuals in two methods

Tab. VI

Species	1967		1968	
	sweep-net	bait	sweep-net	bait
	in per cent			
1. <i>Aedes (Ochlerotatus) maculatus</i>	61.3	76.5	69.1	82.9
2. <i>A. (Aedes) cinereus</i>	22.3	12.4	3.8	3.8
3. <i>A. (Ochlerotatus) punctor</i>	9.5	4.8	19.5	10.9
4. <i>A. (Ochlerotatus) excrucians</i>	2.7	3.5		
5. <i>A. (Ochlerotatus) annulipes</i>	2.0	1.5	1.7	
6. <i>A. (Aedimorphus) vexans</i>	1.2	1.3		2.4
7. <i>A. (Ochlerotatus) flavescens</i>	0.4			
8. <i>Theobaldia (Theobaldia) annulata</i>	0.1		0.4	
9. <i>A. (Ochlerotatus) communis</i>	0.5		5.5	

Taking into consideration the changes in the structure of mosquito communities in the two years of studies few groups of species may be distinguished: 1) maintaining their place in the structure of the community – *A. maculatus* Meig., *A. annulipes* Meig., *Theobaldia annulata* Schr., 2) increasing their share – *A. punctor*, *A. communis*, *A. vexans*, 3) decreasing their share – *A. cinereus* Meig., 4) falling out of the community probably as a result of unfavourable climatic conditions – *A. flavescens*, *A. excrucians*. These different types of reaction of the changing biotope conditions can not be connected with the species abundance in the previous year. They do not depend on this factor and are probably due to the biological and ecological characteristics of species. But in general, the changes in the mosquito fauna during these two years resulting in a decrease of total mosquito number, percentage increase of eurytopic and dominant species in the community, smaller number of species and great mosquito aggregations, point to the advancing drying of the studied area. These two elements – the change of the extent of suitability of the biotope for the mosquitos and the related to it quantitative and qualitative change of the mosquito fauna – decide about the effect of ecotone on the spatial distribution of mosquitos in two basically different situations.

3.3. Analysis of mosquito community from the aspect of the ecotone specificity

The mosquito communities were analysed according to the value of the ecotone for this type of entomofauna. The ecotone examined was the transition zone between the typical biotope, where the mosquitos hatch and stay during the day, and the meadow, without its "own" mosquito fauna, and where they appear periodically.

For the mosquitos, organisms extremely sensitive to environmental conditions, the differences in the vegetation structure producing various microclimatic conditions and different shelter possibilities are the factor determining to a great extent their spatial distribution (Dąbrowska-Prot and Łuczak 1968a). The mosaic structure of the habitat is responsible for the formation of mosquito communities differing in structure and number. As shown by the phytosociological and microclimatic studies the ecotone is a separate unit in the environment creating specific conditions for animals in the undergrowth and herb layer. Furthermore, the ecotone as the contact zone of two different biotopes is a place of abiotic and biotic influences of both biotopes and this should be reflected by the character of the mosquito community there.

As already said, the spatial distribution of mosquitos in the three examined biotopes was very uneven, especially of the fauna of inactive mosquitos, and the worse climatic conditions next year made this unevenness of distribution even greater (Tab. V). Quantitative differences in the mosquito fauna of particular biotopes were very distinct (Tab. VII). In both years of studies the mosquitos were the most abundant in the wet alder wood, then in the ecotone, and they were the less abundant on the meadow. In the dry year the tendency of mosquitos to aggregate in the most suitable for them biotope of alder wood affected their number in the ecotone (in 1967 the number of mosquitos was 3 times smaller than in the alder wood, and in 1968 about 8 times smaller), but still the mosquitos were here much more numerous than on the meadow (in 1967 about 7 times and in 1968 about 10 times).

The differences in the number of particular species in the three examined biotopes were also considerable (Tab. VII). One of the species — *Aedes vexans* — is a definitely ecotone one. In 1967 this species was found mainly in the ecotone, and in 1968 only in the ecotone. Three other species — *A. punctor*, *A. excrucians* and *A. annulipes* — were found on the meadow and in the ecotone in about 50% and mainly in the latter. Other species were either exclusively found in the wet alder wood (*A. communis*, *A. flavescens*, *Th. annulata*) or favoured this biotope to a considerable extent (*A. maculatus*, *A. cinereus*).

Percentage distribution of the whole mosquito fauna and particular species in the three examined biotopes

Tab. VII

Sites	The whole fauna of mosquitoes		<i>Aedes maculatus</i>		<i>A. cinereus</i>		<i>A. punctator</i>		<i>A. communis</i>		<i>A. vexans</i>		<i>A. annulipes</i>		<i>A. excrucians</i>		<i>Theobaldia annulata</i>		<i>A. flavescens</i>		
	1967	1968	1967	1968	1967	1968	1967	1968	1967	1968	1967	1968	1967	1968	1967	1968	1967	1968	1967	1968	
Meadow	bait	3.7	0.8	3.2	1.2	1.9	—	11.5	—	—	—	—	—	5.5	—	4.0	—	—	—	—	—
	sweep-net	4.0	1.2	3.3	1.4	2.1	—	5.2	—	—	—	—	—	—	—	—	—	—	—	—	—
Ecotone	bait	25.0	11.1	20.9	13.5	33.2	11.1	24.1	2.2	—	—	81.8	—	27.8	50	36.0	—	—	—	—	—
	sweep-net	29.3	12.2	28.1	11.8	22.4	—	47.4	—	—	—	33.3	100	33.3	—	33.3	—	—	—	—	—
Alder wood	bait	71.3	88.1	75.9	85.3	64.9	88.9	64.4	97.8	100	100	18.2	—	66.7	50	60.0	—	100	100	100	—
	sweep-net	66.7	86.6	68.6	86.8	75.5	100	47.4	100	—	—	66.7	—	66.7	—	50.0	—	—	—	—	—

Structure of mosquito communities expressed by the percentage of the dominant, subdominant and accessory species

Tab. VIII

Catches Sites	Bait 1967			Sweep-net 1967			Bait 1968			Sweep-net 1968		
	domi- nant	subdom- inant	access- ory species	domi- nant	subdom- inant	access- ory species	domi- nant	subdom- inant	access- ory species	domi- nant	subdom- inant	access- ory species
1 Meadow	53	29.5	17.5	62.5	25.0	12.5	100	—	—	100	—	—
2 Ecotone	51	30.0	19.0	73.3	9.5	17.4	84.6	7.7	7.7	80	20	—
3 Alder wood	65	10.5	24.5	78.8	14.0	7.2	66.8	21.6	11.6	83.1	12.7	4.2
The whole fauna	61.3	22.3	16.4	76.5	12.4	11.1	69.1	19.5	11.4	82.9	10.9	6.2

The changes in the spatial distribution of species on the examined area in 1968 as compared with 1967 were mainly leading to limiting the species occurrence to the alder wood (Tab. VII). The exceptions here is *A. vexans*, which in that year was found only in the ecotone and *A. annulipes*, which was found half and half in the alder wood and ecotone. This choice of the ecotone shows that in the mosquito community there are species mainly connected with this biotope.

Therefore, in each biotope there is a specific mosquito fauna having its own structure (Tab. VIII). In the year with the greater abundance of mosquitoes the structure of the community of active mosquitoes in the ecotone was very much like the structure of the meadow community. In the alder wood, as compared with the other two biotopes, the share of dominant and accessory species was greater. The inactive mosquitoes of these habitats were much more differentiated and none of the biotopes resembled the others. In the year of small mosquito abundance the similarity between the ecotone and meadow no longer existed and each of the biotopes had mosquito communities of a specific structure.

Thus, it can be said, that in good weather conditions and large total mosquito abundance the domination structure of flying mosquitoes in the ecotone resembles the meadow, and the alder wood is a completely separate biotope. In drought conditions and small total mosquito number the meadow is eliminated as a mosquito habitat and the ecotone is the sharp border of the mosquito occurrence. The structure of the inactive mosquitoes in the ecotone is similar to this in the alder wood at both the small and great mosquito abundance.

Analysing the specific structure of mosquitoes of particular biotopes, it can be said that *A. maculatus* was in both years the dominant in active and inactive fauna (Tab. IX). The environmental differences were already observed on the level of the subdominant for: *A. cinereus*, *A. punctor* and *A. vexans*. At great total mosquito abundance *A. cinereus* was the subdominant in the alder wood and ecotone both in active and inactive fauna. On the meadow *A. punctor* was the subdominant in the active mosquito, fauna and *A. vexans* in the inactive fauna.

In the year characterized by small mosquito abundance the biotopes became completely differentiated. In the alder wood *A. punctor* was the subdominant of active and inactive fauna, in the ecotone *A. cinereus* – among the active mosquitoes – and *A. vexans* – among the inactive ones, on the meadow, apart from the dominant *A. maculatus*, no other mosquito species were observed.

In 1967, in all three biotopes, the relative activity of mosquitoes was similar (Tab. X). In 1968 the activity decreased on the meadow and in the alder wood

Percentage of species in the mosquito fauna of particular biotopes

Tab. IX

Species		<i>Aedes maculatus</i>		<i>A. cinereus</i>		<i>A. punctor</i>		<i>A. communis</i>		<i>A. vexans</i>		<i>A. annulipes</i>		<i>A. excrucians</i>		<i>Theobaldia annulata</i>		<i>A. flavescens</i>	
		1967	1968	1967	1968	1967	1968	1967	1968	1967	1968	1967	1968	1967	1968	1967	1968	1967	1968
Meadow	bait	52.8	100	11.8	—	29.4	—	—	—	—	—	3.0	—	3.0	—	—	—	—	—
	sweep-net	62.5	100	6.25	—	6.25	—	—	—	25.0	—	—	—	—	—	—	—	—	—
Ecotone	bait	51.3	84.6	29.5	3.85	9.1	3.85	—	—	3.9	—	2.3	7.7	3.9	—	—	—	—	—
	sweep-net	73.3	80.0	9.5	—	7.8	—	—	—	3.4	20.0	1.7	—	4.3	—	—	—	—	—
Alder wood	bait	64.9	66.8	20.3	3.8	8.5	21.6	0.8	6.3	0.3	—	1.8	1.0	2.3	—	0.2	0.5	0.6	—
	sweep-net	78.8	83.1	14.0	4.2	3.4	12.7	—	—	0.4	—	1.5	—	1.9	—	—	—	—	—

Activity of mosquito in examined biotopes in both years of studies

Tab. X

Year	Meadow					Ecotone					Alder wood				
	The whole fauna	<i>Aedes maculatus</i>	<i>A. cinereus</i>	<i>A. punctor</i>	<i>A. vexans</i>	The whole fauna	<i>A. maculatus</i>	<i>A. cinereus</i>	<i>A. punctor</i>	<i>A. vexans</i>	The whole fauna	<i>A. maculatus</i>	<i>A. cinereus</i>	<i>A. punctor</i>	<i>A. vexans</i>
1967	72.2	69.2	83.3	92.6	0	71.2	63.4	88.5	74.5	73.8	75.6	72.0	81.8	88.6	71.4
1968	66.7	66.7	-	-	1	76.2	73.3	100	100	0	71.6	70.2	72.8	83.3	-

(quite considerably in the former, and less so in the latter), but increased in the ecotone and was the greatest as compared with the other biotopes. Thus, it would mean that this is the zone of intensive penetration of mosquitos in this arrangement of biotopes. This is confirmed by the behaviour of several species in the ecotone – *A. maculatus*, *A. cinereus* and *A. punctor* – the activity of which increased visibly in this biotope in 1968. These species in the alder wood, and also *A. maculatus* on the meadow, were less active that year.

Another striking phenomenon is the great ability of the mosquito *A. vexans* to modify its activity. In alder wood its activity reached 70%, and in less suitable conditions such as on the meadow and in the ecotone this species was quite inactive. None of the species in this area did respond to the environmental conditions by changes in activity to such extent. This property of *A. vexans* had been observed previously (Dąbrowska-Prot 1964). On areas generally unfavourable for mosquitos, *A. vexans* dominated quantitatively and responded the most by a change of activity to the change of the biotope (its activity changed from 0 to 57%). It is possible that its "ecotone" character depends on this property of *A. vexans*.

Seasonal changes in the mosquito fauna of particular biotopes depended both on the quality of these biotopes and on the total number of mosquitos in the given year. At high total number

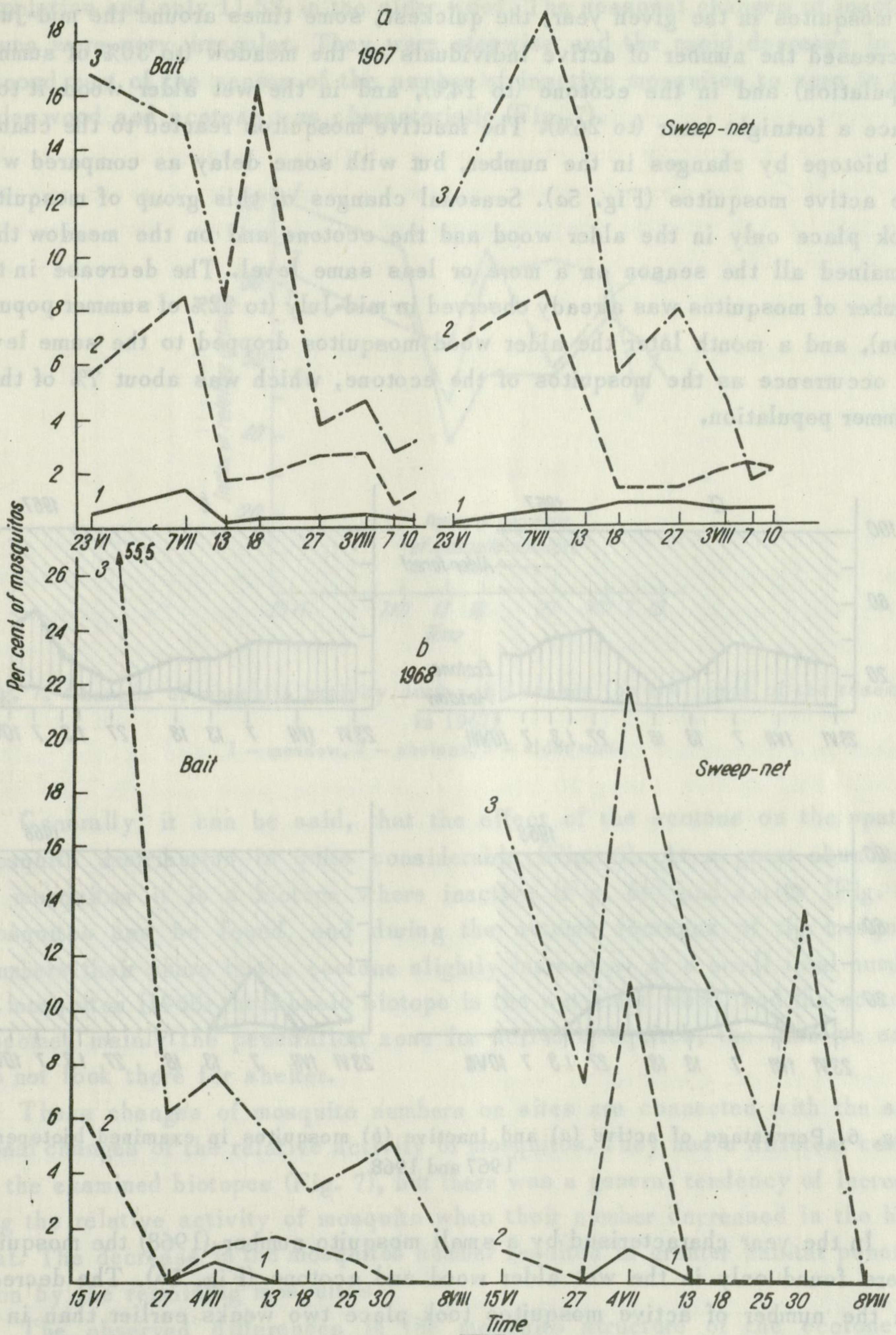


Fig. 5. Seasonal changes of the percentage of mosquito fauna in particular biotopes:
 a - in 1967, b - in 1968
 1 - meadow, 2 - ecotone, 3 - alder wood

of mosquitos in the given year, the quickest, some times around the mid-July, decreased the number of active individuals on the meadow (to 30% of summer population) and in the ecotone (to 14%), and in the wet alder wood it took place a fortnight later (to 26%). The inactive mosquitos reacted to the change of biotope by changes in the number, but with some delay as compared with the active mosquitos (Fig. 5a). Seasonal changes of this group of mosquitos took place only in the alder wood and the ecotone and on the meadow they remained all the season on a more or less same level. The decrease in the number of mosquitos was already observed in mid-July (to 22% of summer population), and a month later the alder wood mosquitos dropped to the same level of occurrence as the mosquitos of the ecotone, which was about 7% of their summer population.

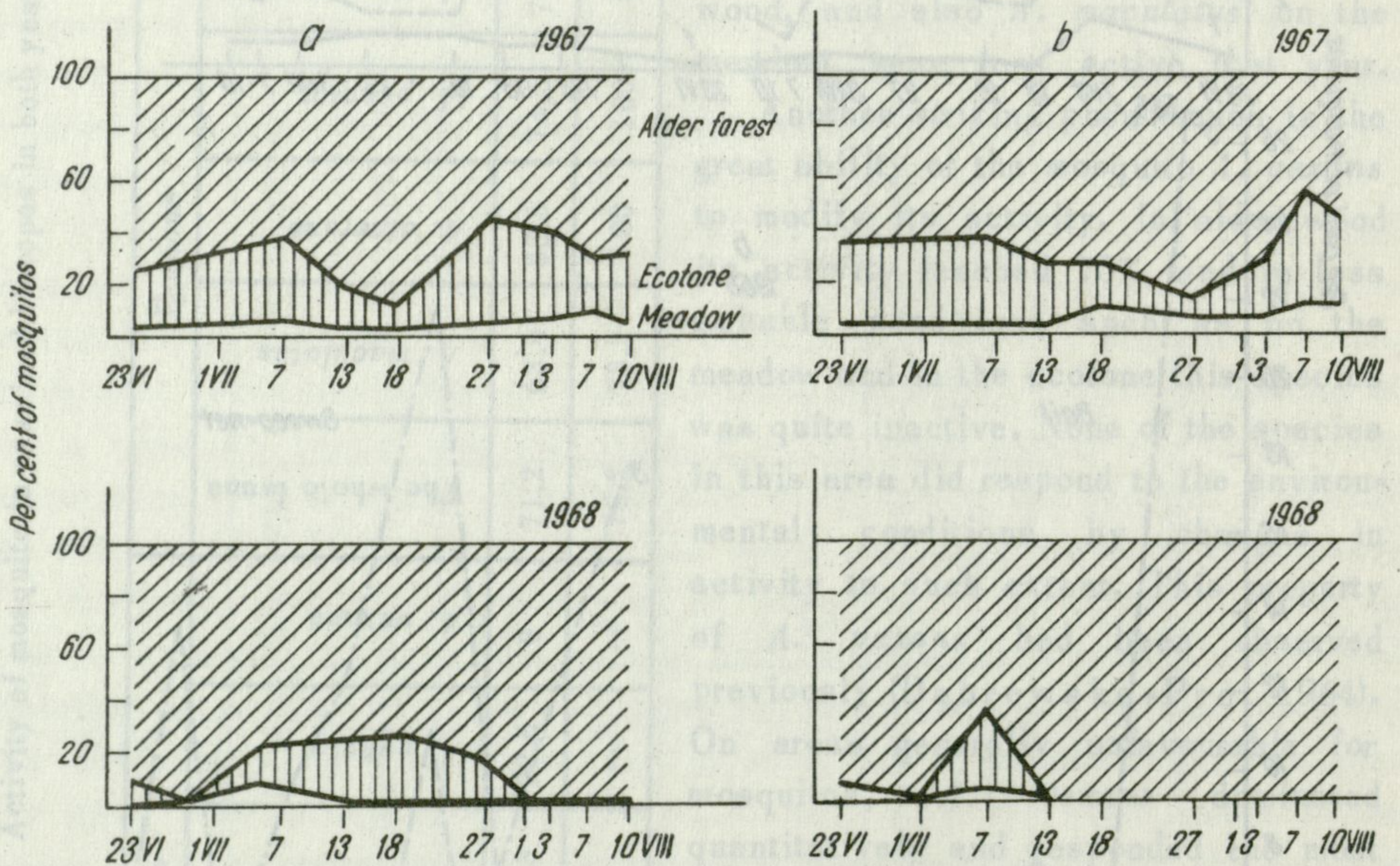


Fig. 6. Percentage of active (a) and inactive (b) mosquitos in examined biotopes in 1967 and 1968

In the year characterised by a small mosquito number (1968) the mosquitos were found only in the wet alder wood and ecotone (Fig. 5b). The decrease in the number of active mosquitos took place two weeks earlier than in the preceding year, and till the end of the studies their number in the alder wood was higher than in the ecotone, although in the latter they were 17% of summer

population and only 11.5% in the alder wood. The seasonal changes of inactive fauna were very irregular. They were stepwise and the rapid decrease in the second part of the season of the number of inactive mosquitos to zero in the alder wood and ecotone was characteristic (Fig. 7).

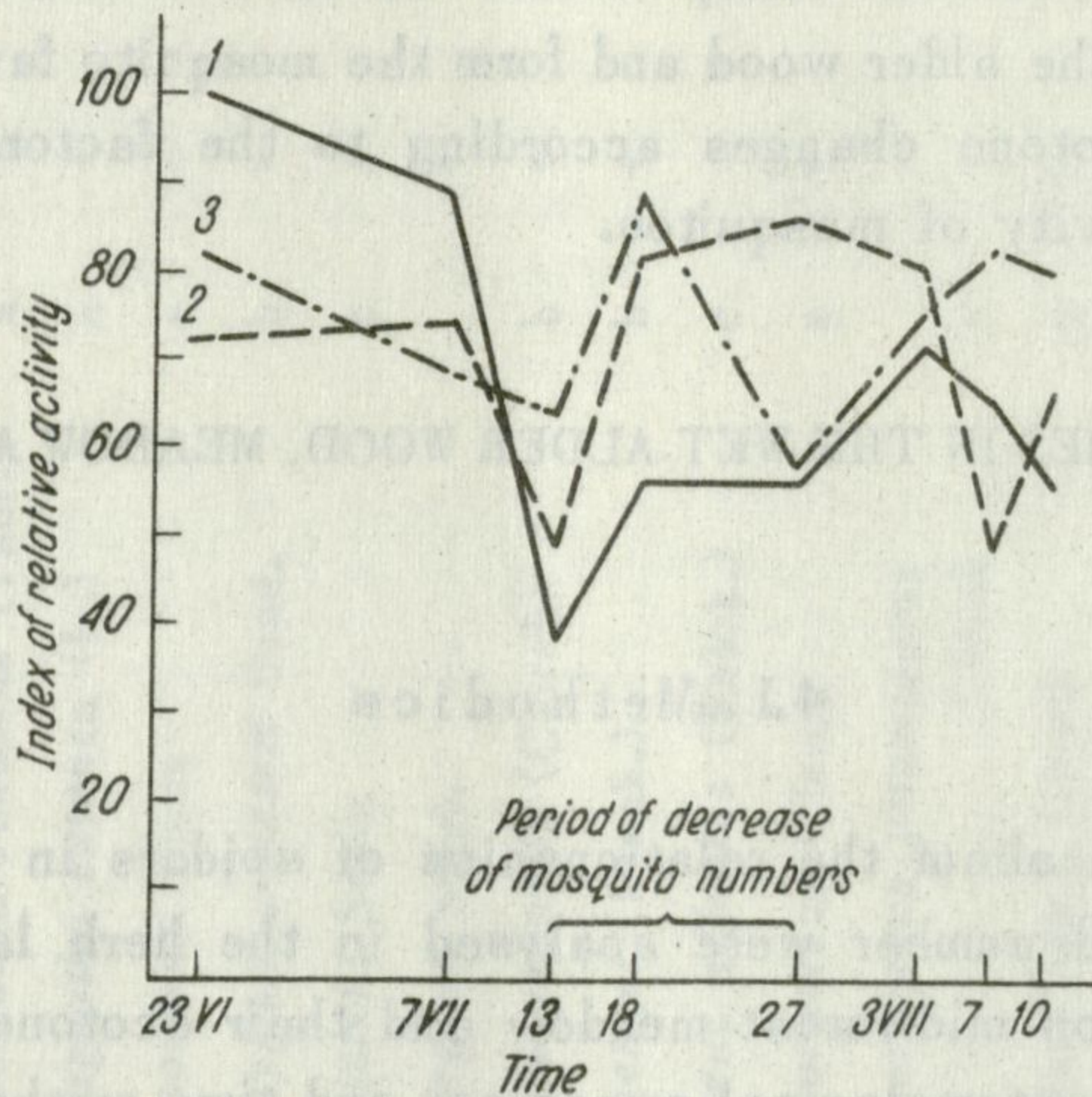


Fig. 7. Changes of mosquito activity during the season (on the basis of the research in 1967)

1 - meadow, 2 - ecotone, 3 - alder wood

Generally, it can be said, that the effect of the ecotone on the spatial mosquito distribution is quite considerable (Fig. 6). At a great abundance of mosquitos it is a biotope where inactive (Fig. 6b) and active (Fig. 6a) mosquitos can be found, and during the autumn decrease of the mosquito numbers their share in the ecotone slightly increases. At a small total number of mosquitos (1968) their basic biotope is the wet alder wood, and the ecotone becomes mainly the penetration zone for active mosquito's, the inactive ones do not look there for shelter.

These changes of mosquito numbers on sites are connected with the seasonal changes of the relative activity of mosquitos. They had a different course in the examined biotopes (Fig. 7), but there was a general tendency of increasing the relative activity of mosquito when their number decreased in the habitat. The decrease in the mosquitos number resulted in greater habitat penetration by the remaining mosquitos.

The observed differences in the mosquito structure of the ecotone as compared with the neighbouring biotopes, their seasonal dynamics and activity show that the ecotone is for the mosquitos clearly marked and different from

the biotopes it originates from. The role of this biotope is closely connected with the basic feature of mosquito behaviour – mobility. The ecotone is a place of intensive exchange of mosquitos between the contact biotopes at a greater mosquito number. In unsuitable climatic conditions and at a small mosquito number the ecotone is the sharp border of their occurrence. Only active individuals fly from the alder wood and form the mosquito fauna of the ecotone. The role of the ecotone changes according to the factors determining both the density and activity of mosquitos.

4. SPIDER COMMUNITIES IN THE WET ALDER WOOD, MEADOW AND THEIR ECOTONE

4.1. Methodics

In order to learn about the relationships of spiders in the transition zone their occurrence and number were analysed in the herb layer and on shrubs in the alder wood, on mid-forest meadow and their ecotone. Two quantitative methods were used: entomological sweep-net and time method. As a representative sample was regarded the one with 25 sweep-net strokes over plants in 10 series, the second method meant collecting spiders by looking out the spiders in a determined time unit. In 1967 the sweep-net method and the method of collecting spiders during 30 min. in each biotope, were used. In 1968 only the method of "looking out" was used and the accepted unit of time was one hour. From June to September 7 sweep-net samples and 7 samples by "looking out" were taken in 1967, and 7 samples by "looking out" in 1968. The analysis of the material showed the rightness and the profits of using both these quantitative methods as the species associated with plants fall in different proportions into the entomological sweep-net, and *vice versa*, not all of them can be easily "looked out". However, both methods basing on the sweep-net in analyses of quantitative variability (Łuczak 1958, Łuczak and Wierzbowska 1959) complete one another giving a complete picture of the number relations in spider communities in the herb layer of examined biotopes.

4.2. General description of the spider communities

In all three examined biotopes, during two years of the studies, 74 spider species of herb layer and shrubs belonging to 12 families were found (Tab. XI). At least 6 young stages not identified to the species were found, which altogether makes 80 species associated with plants. The most numerously repre-

Spiders collected in examined biotopes

Tab. XI

Species		Alder- wood	Ecotone	Meadow	Species		Alder- wood	Ecotone	Meadow
<i>Dictyna arundinacea</i> (L.)				+	<i>Achaearanea simulans</i> (Thor.)	a	+	+	+
<i>D. uncinata</i> Thor.	b	+	+		<i>Tetragnatha extensa</i> (L.)	a	+	+	+
<i>Clubiona lutescens</i> Westr.	b	+	+		<i>T. montana</i> Simon	a	+	+	+
<i>C. terrestris</i> Westr.	b	+	+		<i>Pachygnatha listeri</i> Sund.	b	+	+	
<i>C. reclusa</i> Cambr.	c		+	+	<i>P. clercki</i> Sund.	b	+	+	
<i>C. germanica</i> Thor.			+		<i>P. degeeri</i> Sund.		+		
<i>C. subtilis</i> (L. Koch)			+		<i>Meta segmentata</i> (Clerck)	b	+	+	
<i>Cheiracanthium erraticum</i> (Fabr.)	c		+	+	<i>M. mengei</i> (Black.)	b	+	+	
<i>Micrommata virescens</i> (Clerck)	a	+	+	+	<i>Araneus adiantus</i> (Walck.)	c		+	+
<i>Misumena vatia</i> (Clerck)				+	<i>A. marmoreus</i> Clerck	a	+	+	+
<i>M. tricuspidata</i> (Fabr.)	c		+	+	<i>A. marmoreus pyramidatus</i> Clerck	a	+	+	+
<i>Diaea dorsata</i> (Fabr.)		+		+	<i>A. diadematus</i> Clerck	a	+	+	+
<i>Oxyptila brevipes</i> (Hahn)		+			<i>A. cucurbitinus</i> (Clerck)	a	+	+	+
<i>O. atomaria</i> (Panzer)			+		<i>A. redii</i> (Scopoli)	c		+	+
<i>Xysticus cristatus</i> (Clerck)	c		+	+	<i>A. quadratus</i> Clerck	c		+	+
<i>X. ulmi</i> (Hahn)	a	+	+	+	<i>A. sturmi</i> (Hahn)		+		
<i>X. bifasciatus</i> C.L.Koch				+	<i>A. alsine</i> (Walck.)		+		
<i>Philodromus rufus</i> Walck.		+			<i>A. patagiatus</i> (Clerck)				+

Species	Alder-wood	Ecotone	Meadow	Species	Alder-wood	Ecotone	Meadow
<i>Ph. aureolus</i> (Clerck)			+	<i>Mangora acalypha</i> (Walck.)	a	+	+
<i>Ph. emarginatus</i> (Schrank)		+		<i>Cyclosa oculata</i> (Walck.)	b	+	
<i>Tibellus oblongus</i> (Walck.)	c	+	+	<i>Singa pygmaea</i> (Sund.)			+
<i>Thomisus</i> sp.		+		<i>S. hamata</i> (Clerck)	c	+	+
<i>Evarcha arcuata</i> (Clerck)	c	+	+	<i>Theridiosoma gemmosum</i> (L.Koch)	+		
<i>E. falcata</i> (Clerck)		+		<i>Oedothorax gibbosus</i> (Black.)	+		
<i>Heliophanus</i> sp.			+	<i>Erigone longipalpis</i> (Sund.)	+		
<i>Lycosa</i> sp.	+			<i>E. atra</i> Black.		+	
<i>Pirata</i> sp.	+			<i>Gongylidium rufipes</i> (L.)	b	+	+
<i>Trochosa</i> sp.	+			<i>Gonatium rubellum</i> (Black.)	b	+	+
<i>Dolomedes fimbriatus</i> (Clerck)	a	+	+	<i>Bathyphantes nigrinus</i> (Westr.)	b	+	+
<i>Pisaura mirabilis</i> (Clerck)	a	+	+	<i>Helophora insignis</i> (Black.)	b	+	+
<i>Agelena similis</i> (Menge)	c	+	+	<i>Linyphia clathrata</i> (Sund.)	b	+	+
<i>Theridion pictum</i> (Walck.)	a	+	+	<i>L. triangularis</i> (Clerck)	a	+	+
<i>Th. ovatum</i> (Clerck)	a	+	+	<i>L. hortensis</i> (Sund.)	+		
<i>Th. varians</i> Hahn	+			<i>L. montana</i> (Clerck)	a	+	+
<i>Th. bimaculatum</i> (L.)	c	+	+	<i>L. pusilla</i> (Sund.)			+
<i>Th. impressum</i> L. Koch			+	<i>Floronia bucculenta</i> (Clerck)	b	+	+
<i>Enoplognatha schaufussi</i> (L.Koch)			+	<i>Prolinyphia peltata</i> (Wider)	+		

a — species common for the three biotopes, b — species common for the ecotone and forest, c — species common for the ecotone and meadow; species caught only in one biotope do not have a mark.

sented were the families *Argiopidae* (18 species), *Linyphiidae* (14 species) and *Thomisidae* (13 species) forming 56% of all caught species. In the alder wood 45 species were found, on the meadow 46 and in the ecotone 52 (Tab. XII). The *Argiopidae* and *Linyphiidae* dominated in the forest, the *Argiopidae* in the ecotone and the *Argiopidae* and *Thomisidae* on the meadow.

Number of families, number of species and the total number of spiders in the examined biotopes (on the basis of quantitative samples taken with a sweep-net and by "looking out")

Tab. XII

Biotopes	Number of families	Number of species	Number of individuals		Total
			sweep-net	"looking out"	
1967			0.5 h.		
Alder wood	11	45	1288	517	1805
Ecotone	12	52	1477	519	1996
Meadow	11	46	1528	352	1880
					5681
1968			1 h.		
Alder wood	7	22		744	744
Ecotone	9	30		641	641
Meadow	10	33		540	540
					1925

The species composition of the three examined biotopes is compared using the similarity coefficient of Sørensen (QS) according to the formula:

$$QS = \frac{2c}{a+b} \times 100$$

where: a — number of common species, b — number of species in one biotope, c — number of species in the other biotope.

The similarity coefficient between the alder wood and the adjoining mid-forest meadow is 26%, which points to a small number of common species (1/4); comparing the alder forest and its ecotone the coefficient is 50%, and comparing the meadow and the ecotone it is 45%. This means that the transition zone has a considerable number of species common with the forest and the meadow and despite this differs visibly from both these typical habitats. More thorough analysis shows that the spider fauna in the transition zone is a mixture of

“forest” and “meadow” species and all the scarce species common both for the meadow and forest also are found in the ecotone.

In 1967, using both methods, 5681 spiders were collected, in 1968, using the “looking out” method – 1925 (Tab. XII). The majority of spiders were found in the ecotone. Figure 8 illustrates the percentage of various spider groups in the alder wood, meadow and ecotone in 1967 and 1968.

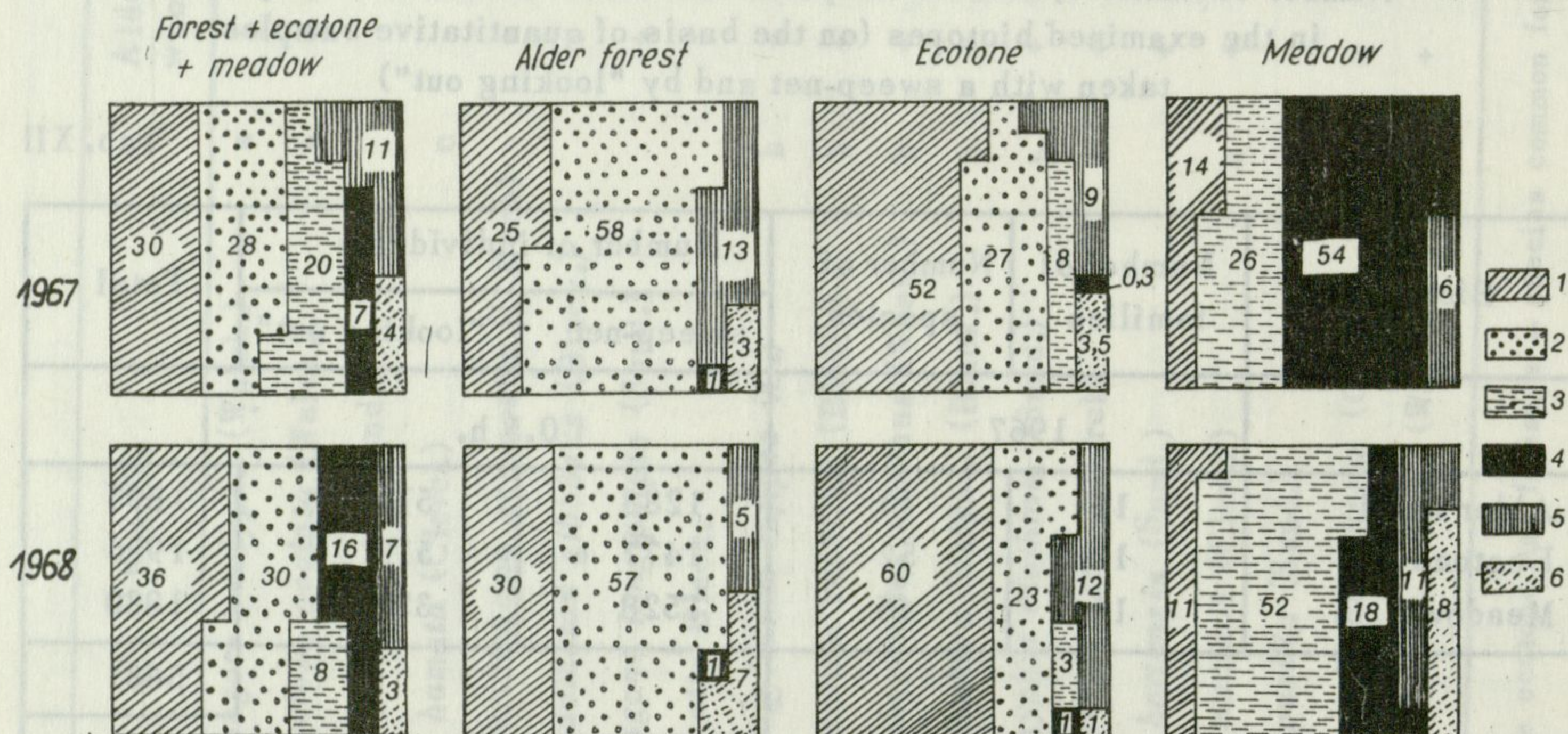


Fig. 8. Abundance (in per cent) of particular groups of spider species in the examined biotopes

1 – species common for the three biotopes, 2 – species common for two biotopes (forest, ecotone), 3 – species common for two biotopes (meadow, ecotone), 4 – species exclusive for particular biotopes, 5 – species with an indicated genus only, 6 – destroyed spiders; square = 100% = total number abundance

In the collected spider material 4 groups of species are distinguished. These are:

1. Species common for all three biotopes – 16 (Tab. XI). They are 30% of all spiders collected in 1967 from all three biotopes together, and 36% in 1968. These are not ecologically uniform species, some of them prefer the alder wood, some are more numerous found on the meadow or in the ecotone. To this last group belong all species called the “ecotone” ones in this paper, which means species having the greatest density in the ecotone (see below).

2. Species common for only two biotopes, namely the forest and ecotone (Tab. XI). There are 14 species and they are altogether 28% of the total number of spiders collected in 1967, and 30% of those collected in 1968.

3. Species common only for the meadow and ecotone (Tab. XI). There are 12 species and their number was 20% of all collected spiders in 1967, and 8% in 1968.

4. Species collected only in one biotope. There are 32 such species: 13 caught in the alder wood, 9 in the ecotone and 10 on the meadow. In the alder wood and the ecotone all the species were caught singly or in a small number, the 6 species caught on the meadow belonged to those abundant ones.

The shares of these groups of species in the total number of collected spiders in examined biotopes in 1967 and 1968 are given in Figure 8.

4.3. Spider communities of the ecotone against the background of the examined biotopes

4.3.1. Ecotone species

In the examined ecotone, as already mentioned, there are spider species living in the alder wood and on the mid-forest meadow. Apart from the typical forest and meadow species there is a group of species having a greater density in the ecotone than in the typical biotopes. These are: *Linyphia triangularis*, *Theridion ovatum*, *Araneus marmoreus*, *A. diadematus*, *Dolomedes fimbriatus* and *Tetragnatha extensa*. All these species belong to the group of species common for the three biotopes, and are 52–60% of all individuals found in the ecotone. Depending on their ecological requirements beyond the ecotone they are either more numerous in the forest or on the meadow. The ecotone species preferring the forest are *L. triangularis* and *Th. ovatum*, whereas to those preferring the herbage-meadow belongs *A. marmoreus*. This is shown by a comparison of the numbers of these spiders obtained in comparable quantitative samples from the three biotopes (Tab. XIII). *D. fimbriatus* was found in similar numbers in the forest and on the meadow. Other species – *A. diadematus* and *T. extensa* – were caught in such a small number in the typical biotopes that it could not be determined, which biotope apart from the ecotone is the preferred one.

The greatest abundance of these species in the ecotone was observed in both years in the material collected using "looking out" method (Tab. XIII). If the number of spiders of each species, caught in the three biotopes, is 100%, then in 1967 in the ecotone we had: *L. triangularis* – 60%, *A. diadematus* – 64%, *Th. ovatum* – 70%, *D. fimbriatus* – 62%, *A. marmoreus* (both forms) – 64%, *T. extensa* – 77%, and in 1968: 54%, 70%, 55%, 64%, 54%, 54%, respectively. Still, this does not mean that the density of these species is always similar in the ecotone of similar biotopes. In the previous paper on the ecotone of alder wood and mixed forest (Dąbrowska-Prot and

Species common for the three examined biotopes

Tab. XIII

Species	Numbers in comparable samples in 1967			Total
	alder wood	ecotone	meadow	
<i>Linyphia triangularis</i>	206	307	3	516
<i>Theridion ovatum</i>	130	328	9	467
<i>Dolomedes fimbriatus</i>	56	171	48	275
<i>Araneus marmoreus</i>	19	78	47	144
<i>A. marmoreus pyramidatus</i>	1	44	1	46
<i>A. diadematus</i>	19	43	5	67
<i>Tetragnatha extensa</i>	3	31	6	40
<i>T. montana</i>				
<i>Xysticus ulmi</i>	2	8	95	105
<i>Mangora acalypha</i>	1	13	16	30
<i>A. cucurbitinus</i>	6	4	3	13
<i>Th. pictum</i>	2	5	1	8
<i>Achaearanea simulans</i>				
<i>Pisaura mirabilis</i>				
<i>Micrommata virescens</i>	1	3	1	5
Numbers in comparable samples in 1968				
<i>Theridion ovatum</i>	64	112	28	204
<i>Linyphia triangularis</i>	110	131	1	242
<i>Dolomedes fimbriatus</i>	14	30	3	47
<i>Araneus marmoreus</i>	4	51	5	60
<i>A. marmoreus pyramidatus</i>	11	5	28	44
<i>A. diadematus</i>	16	56	8	80
<i>Th. pictum</i>	5	3	1	9
<i>L. montana</i>	2	5	1	8

Łuczak 1968a) it was found that only *L. triangularis* was the ecotone species. This phenomenon depends on the arrangement of biotopes, the ecotone of which, depending on its character (i.e. microclimatic conditions and vegetation structure of great significance for the distribution of spiders), may play a different part towards the species on neighbouring biotopes.

The number dynamics of ecotone species in both years of studies showed the greatest density in the ecotone during the entire vegetation season. *L. triangularis* and *Th. ovatum* are good examples of the seasonal dynamics of ecotone spiders. The abundance of *L. triangularis* examined by the sweep-net method and by "looking out" is rather greater in the ecotone than in alder wood (Fig. 9). *Th. ovatum* is also during the entire vegetation season

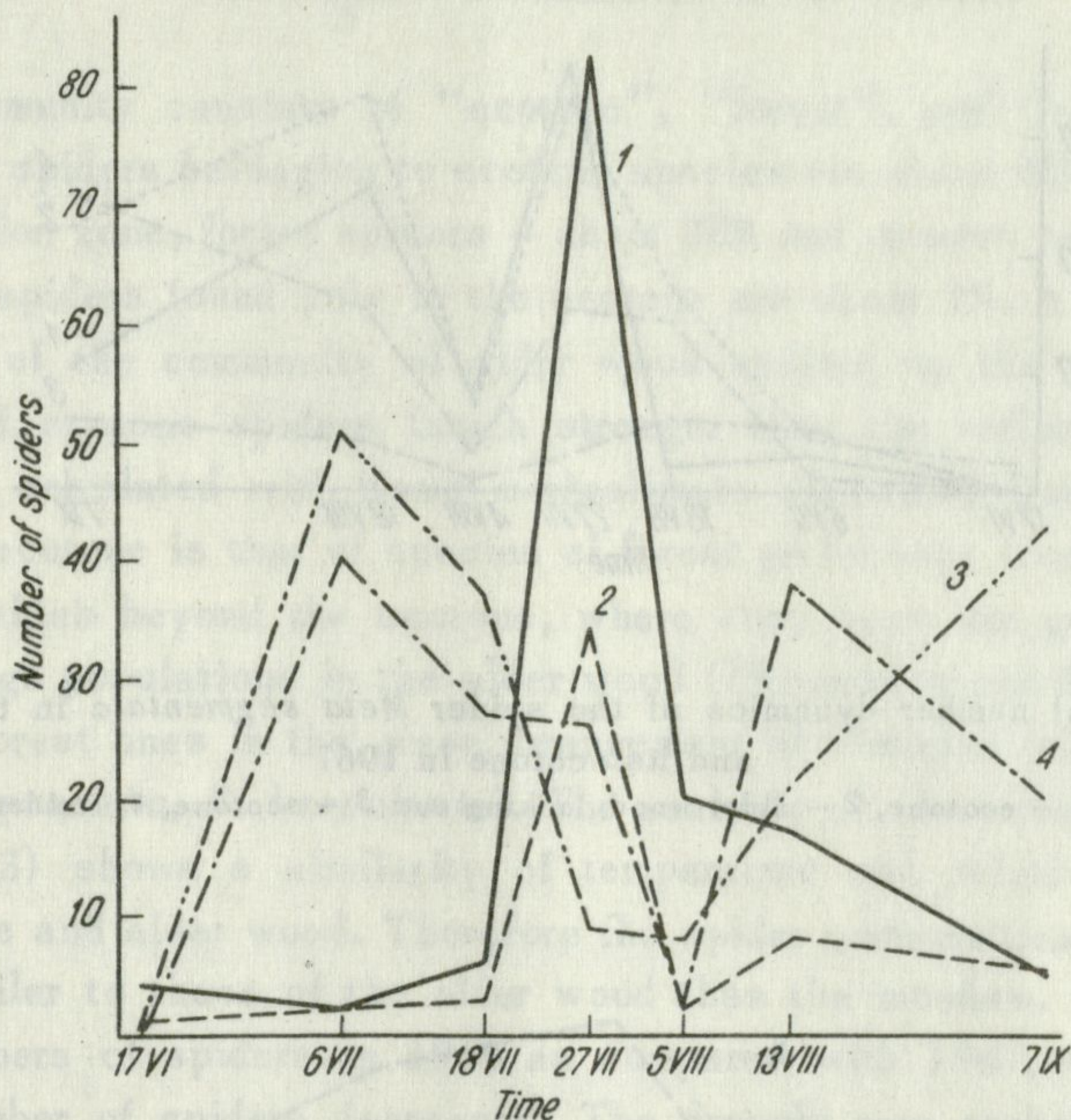


Fig. 9. Seasonal number dynamics of the spider *Linyphia triangularis* in the alder wood and ecotone in 1967

sweep-net: 1 - ecotone, 2 - alder wood; "looking out": 3 - ecotone, 4 - alder wood

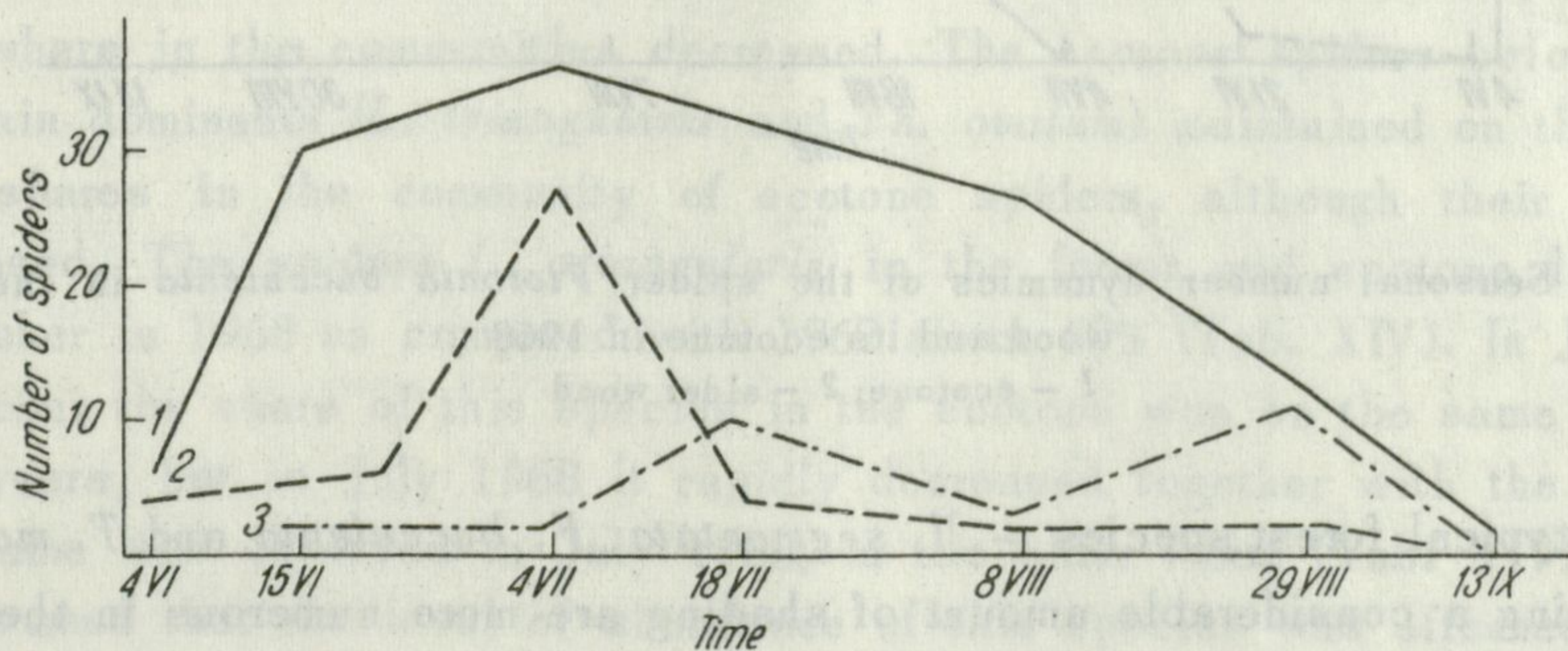


Fig. 10. Seasonal number dynamics of the spider *Theridion ovatum* in three examined biotopes in 1968

1 - ecotone, 2 - alder wood, 3 - meadow

the most numerous in the ecotone, less numerous in the forest, and the least numerous on the meadow (Fig. 10).

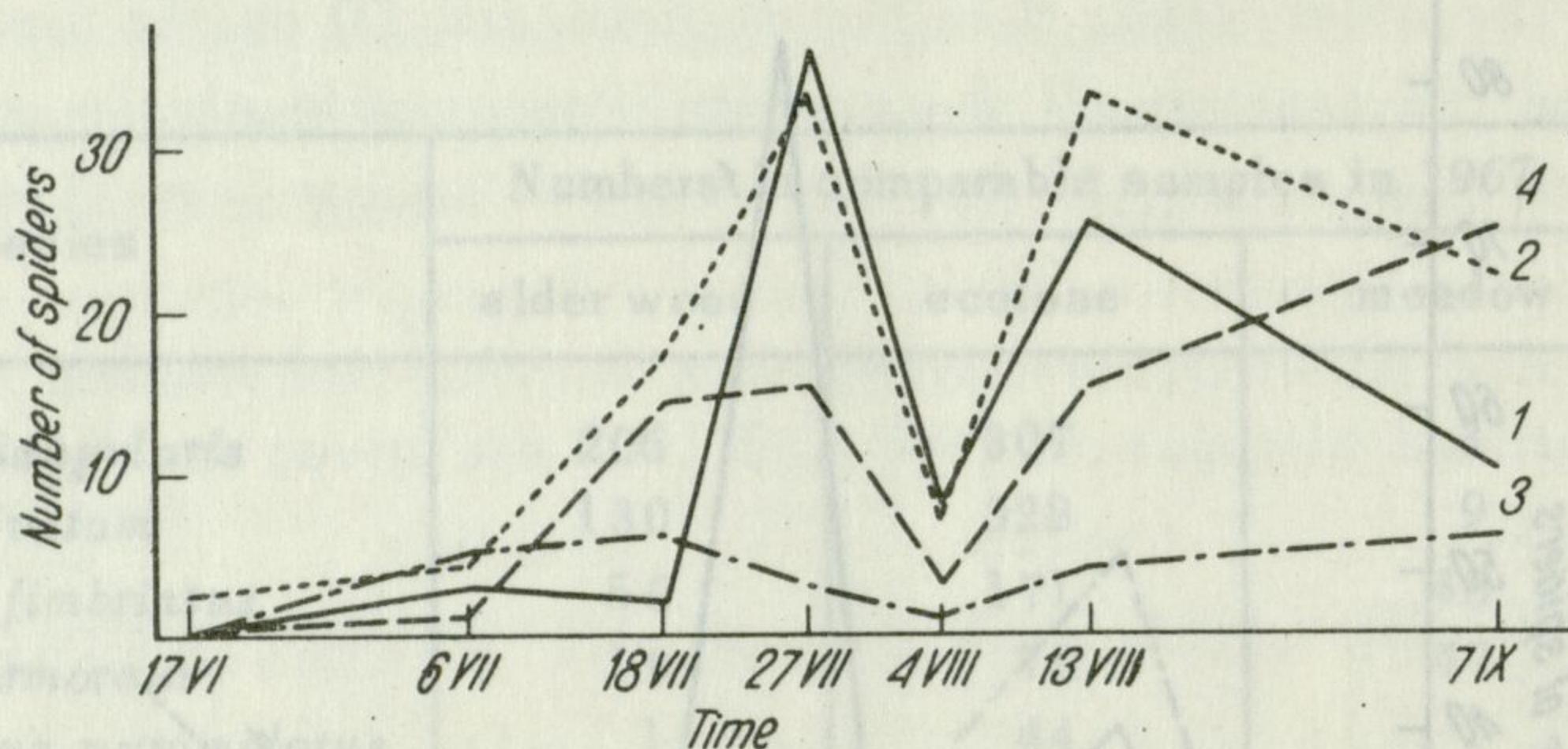


Fig. 11. Seasonal number dynamics of the spider *Meta segmentata* in the alder wood and its ecotone in 1967

sweep-net: 1 - ecotone, 2 - alder wood; looking out: 3 - ecotone, 4 - alder wood

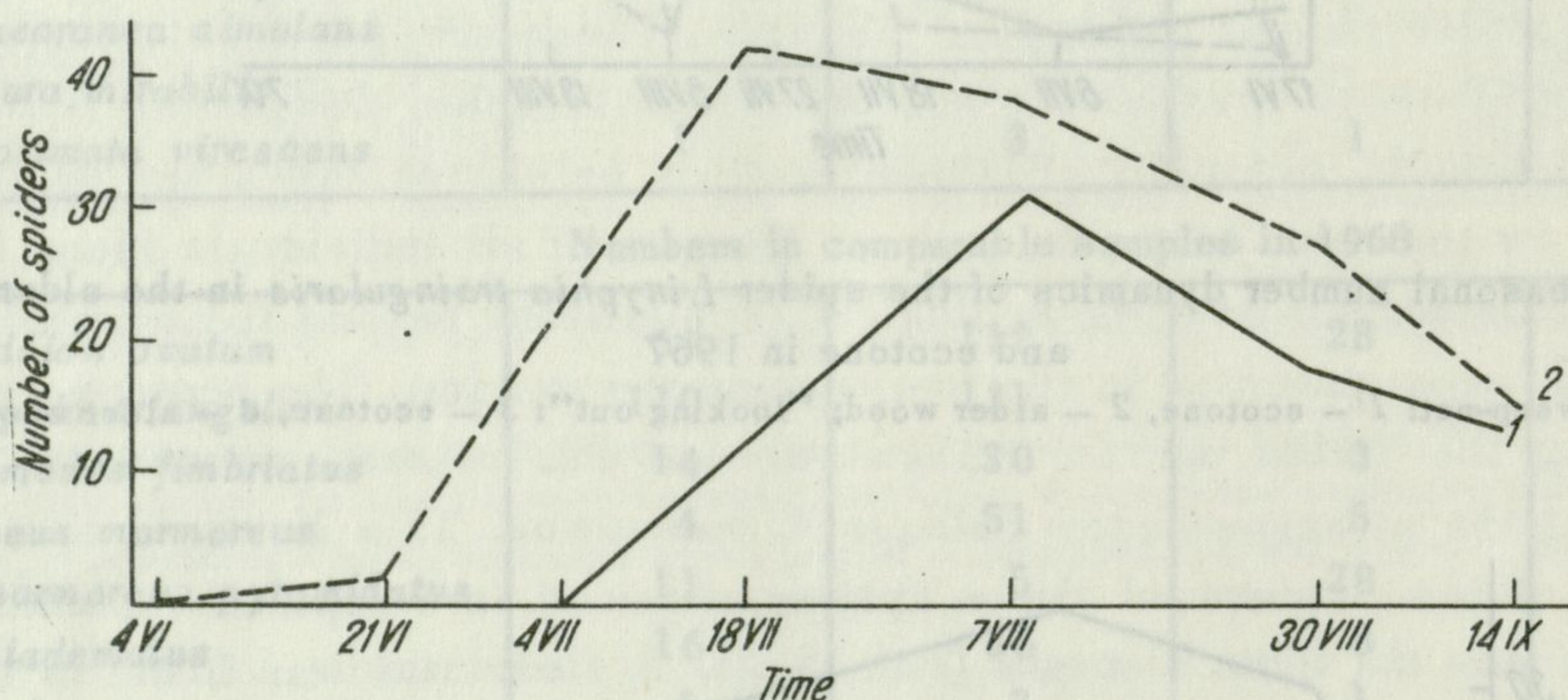


Fig. 12. Seasonal number dynamics of the spider *Floronia bucculenta* in the alder wood and its ecotone in 1968

1 - ecotone, 2 - alder wood

The typical forest species - *M. segmentata*, *F. bucculenta* and *T. montana* - requiring a considerable amount of shading are more numerous in the alder wood (Fig. 11, 12). The dominant meadow species are so scarce in the ecotone that the curves of the number dynamics in both biotopes can not be compared. They are very numerous on the meadow during the whole season, or at least in its greater part.

The factor differentiating the three biotopes is the insolation, and therefore such light requiring meadow species as, e.g., *Linyphia pusilla*, *Tibellus oblongus*, *Araneus quadratus* and some others are not found in the ecotone.

4.3.2. Spider communities in the ecotone

This community consists of "ecotone", "forest", and "meadow" spider species. The spiders belonging to ecotone species are about 60% of all spiders of the transition zone, forest spiders – about 30% and meadow ones – about 9%, whereas the spiders found only in the ecotone are about 1%. A great influence is observed of the community of alder wood spiders on the structure of the community of ecotone spiders (much stronger than the influence of meadow spiders) and correlated with some microclimate elements. Quite considerable share in the ecotone is that of species of forest preference (considered above), i.e., such, which beyond the ecotone, where they have the greatest density, have also large populations in the alder wood (*Th. ovatum* and *L. triangularis*), and typical forest ones in the given arrangement of biotopes (e.g. *Pachygnatha listeri*, *M. segmentata*, *F. bucculenta*). The analysis of microclimatic conditions (Section 2.4.3) shows a similarity of temperature and relative air humidity in the ecotone and alder wood. Therefore the spider communities of the ecotone are more similar to those of the alder wood than the meadow.

The numbers of spiders in 1968 as compared with 1967, change. In 1968 the total number of spiders decreased. The drought was probably responsible for this phenomenon as it started in 1967 and as the analyses of microclimate show, became even worse in 1968. In the summer 1968 the maximal daily relative air humidity decreased even more than in 1967. In the alder wood only about 72% of spiders found in 1967 were caught, in the ecotone about 73%, and on the meadow about 77%. Several species decreased in number and also their share in the communities decreased. The ecotone spiders belonging to the main dominants (*L. triangularis* and *Th. ovatum*) maintained on the whole their shares in the community of ecotone spiders, although their numbers decreased. The spiders *L. triangularis* in the forest and ecotone decreased in number in 1968 as compared with 1967 about 60% (Tab. XIV). In June and September the share of this species in the ecotone was on the same level in both years, but in July 1968 it rapidly decreased together with the number. The same was observed in July 1968, in the alder wood (Tab. XIV). It can be assumed that the level of abundance of this species was affected by the weather in spring and summer in 1968 and the drought affected the most the summer *L. triangularis* population.

The number of *Th. ovatum* in the ecotone decreased in 1968 about 45% (Tab. XIV), but maintained its position in the spider community as compared with 1967. In the alder wood its number and share were similar in both years, the greatest share in the late spring, smaller in July, and very slight in August. This means that *Th. ovatum* is "ecologically stronger" in the community

Number of spider species in 1967 and 1968
in the ecotone and alder wood (after the "looking out" method)

Tab. XIV

Species	Number		Decreased	Increased
	1967	1968	in %	in %
Ecotone				
<i>Linyphia triangularis</i>	332	131	60	
<i>Theridion ovatum</i>	200	112	45	
<i>Floronia bucculenta</i>	20	60		68
<i>Dolomedes fimbriatus</i>	22	30		27
<i>Tetragnatha montana</i>	6	17		65
<i>Araneus marmoreus</i>	16	56		70
<i>Meta segmentata</i>	44	44	—	—
<i>A. diadematus</i>	56	56	—	—
Alder wood				
<i>Linyphia triangularis</i>	302	110	64	
<i>Theridion ovatum</i>	44	64		31
<i>Floronia bucculenta</i>	140	146	—	—
<i>Dolomedes fimbriatus</i>	6	14		57
<i>Tetragnatha montana</i>	76	91		16
<i>Araneus marmoreus</i>	30	15	50	
<i>Meta segmentata</i>	146	106	27	
<i>A. diadematus</i>	20	16	20	
<i>Achaearanea simulans</i>	52	60		13

of ecotone spiders than in the alder wood ones in this arrangement of biotopes, because even in the worse climatic conditions in the very dry year it still maintained its high share in the community of ecotone spiders. This is a classically "ecotone" species, because its density in the transition zone is much greater than in the alder wood, and the differences in the intensity of its occurrence in these two biotopes are sharper than in *L. triangularis*.

The vegetation structure of the ecotone is more like the structure of meadow vegetation than the forest one, because of the lack of tree layer and small number of shrubs. Furthermore, the herb layer, from which the spiders are collected, although very high and rather dense, shows considerable differences. The ecotone vegetation is slightly lower (usually 50–80 cm) and the dense ground layer 20–30 cm high visibly stands out. But in the wet alder wood there are many plants even 1 m high and many low ones, even trailing on the ground.

Still the plants of an average height fill more or less evenly the whole space of this vegetation layer. This aspect of vegetation structure is important for web spiders, which weave their webs on different heights. Observations allow to determine the most frequent height of these webs. And so, e.g., high on the herb layer there are usually webs of *T. montana* and overgrown *Meta segmentata*. Perhaps these species prefer the forest only because of the high plants in the herb layer. Another typical forest species *F. bucculenta*, which spreads the webs lower, on the level of *L. triangularis* (which in other biotopes such as, e.g., young pine forest, can build webs high on the pine trees), settles less numerously than the latter in the ecotone. It seems that in this instance the microclimatic conditions are more important as well as the great capacity of alder wood biotope, which allows for this species, weaker in competition with *L. triangularis*, to settle the accessible and spare ecological niches. The ecotone does not have so many niches because of the simpler vegetation structure. Anyway, it can be assumed that the differences of vegetation structure affect the differences in the structure of spider communities (Duffey 1962).

In July 1968, in the alder wood, probably due to the weaker position of *L. triangularis* (decrease of abundance), the species *F. bucculenta* increased its share reaching the place of the first dominant, and *A. simulans* also increased its share. *L. triangularis* and *F. bucculenta* belong to species of a similar ecological niche. It is quite possible that between these species there is a competition as they build similar webs on the same height and in the same forest layer (both belong to the *Linyphiidae* family) and catch the same type of prey.

A comparison of the number dynamics of spiders in examined biotopes shows that in early autumn the abundance of almost all spider species decreases (Fig. 13). This phenomenon on such a scale is neither observed in that period in the forest nor on the meadow. Even *P. listeri*, which greatly increases in abundance at the beginning of September in the alder wood, becomes also less numerous in the ecotone. This is probably the effect of drought, which in autumn destroys the ecotone environment quicker than the forest. In the Chapter describing the microclimate (2.4.3) it is said that in the herbage of the transition zone some dicotyledons and *Poa trivialis* started to wither already in August. In September green plants began to dry up, and this process took place first in the ecotone and then in the alder wood. Therefore, the conditions as regarding the humidity and vegetation structure became worse, and especially in the ecotone zone. This resulted in quicker than in the alder wood reduction of spiders.

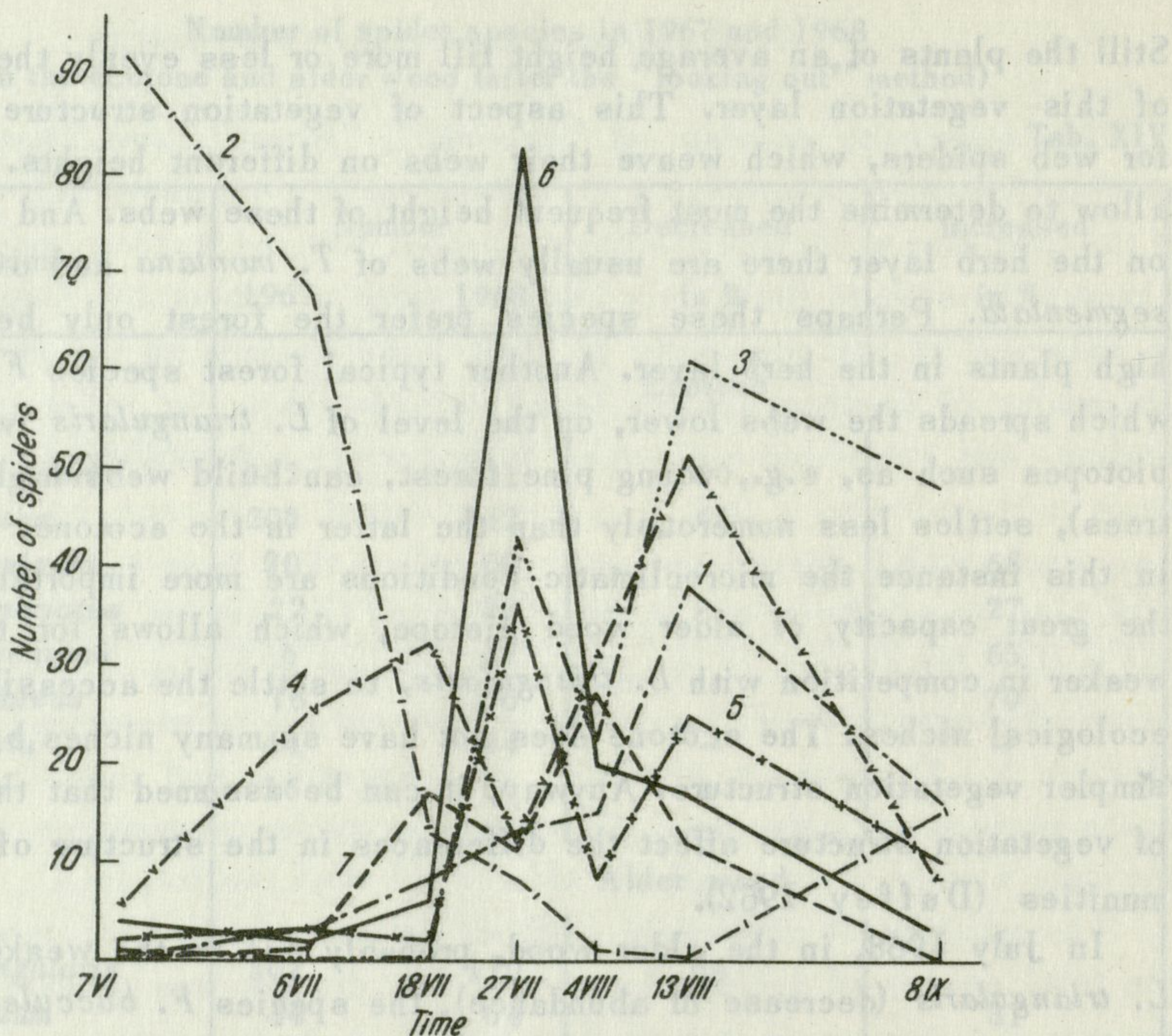


Fig. 13. Number decrease of 6 spider species in the ecotone from 13 August 1967
 1 - *Tetragnatha montana*, 2 - *Theridion ovatum*, 3 - *Pachygnatha listeri*, 4 - *Dolomedes fimbriatus*, 5 - *Meta segmentata*, 6 - *Linyphia triangularis*, 7 - *Araneus marmoreus*

It is worth pointing out that in the summer 1967 a greater number of species was found in the ecotone (36) than in the forest (26) and on the meadow (25).

5. DISCUSSION

The studies on the ecology of mosquitos and spiders have been conducted on the strict border of the biotopes and plant formations: forest-meadow. The transition zone is the area, where the floristic similarity to the forest and the meadow is less than 50% (Fig. 2 A, B). As it can be seen, the wide strongly shaded part of the transition zone (diagram A9) is floristically more similar to the forest, and the narrow, in better light (diagram B) is more similar to the meadow. From the phytosociological point of view this is a herbage meadow belonging to *Filipendulo-Petasition* of the *Molinietalia* order (periodically wet meadows).

But, where our studies are concerned, the physiognomical differences of plant communities depending on the floristic composition are of greater importance, and first of all the life form of species deciding about the plant formations (here forest and grass). In adjacent, but completely different plant communities (wet alder wood and much drier, insolated meadow) the living conditions of the examined group of arthropods were quite different. Although the herbage vegetation of the transition zone belonged to the class of meadow communities, the life conditions of the arthropods in the biotope were not similar to the conditions on the examined meadow through a greater part of the vegetation season. First of all the transition zone was strongly affected by the shade from the forest facing the south and thus the conditions were similar to forest ones. Furthermore, large dicotyledonous plants prevailed in this zone (as opposed to the grassy meadow) and shaded this biotope even more thus creating a quieter and more moist life habitat in late spring and summer. (This explains, e.g., the greater similarity of the community of ecotone spiders to that of the alder wood than to the meadow one). This situation changed in autumn, when after the drying up of leaves the community was much less dense. The life conditions in the ecotone changed thus during the day and the vegetation season depending on the time of insolation and angle of solar rays, and therefore the range of irradiance and from one year to another, depending on the weather conditions (mainly the amount of precipitation).

The plant community developing in the transition zone is typical for the wet alder wood margins, and therefore is a typical ecotone community. The greatest share is of the moisture-requiring species occurring to the same extent in forest and meadow associations: *Poa trivialis*, *Deschampsia caespitosa*, *Filipendula ulmaria*. A high share have also some forest species such as *Urtica dioica* and meadow species: *Veronica chamaedrys* and *Rumex acetosa*. The most "ecotone" species in this transition zone is *Calamagrostis lanceolata*, which in the deep part of wet alder wood is found only in the gaps in the forest stand and in the thickets. The tree most attached to the examined ecotone is *Betula pubescens*, which has the right water conditions in between the wet forest and dry meadow.

Undoubtedly, for mosquitos the ecotone differs from wet alder wood and the meadow. This is visible in the differences of the mosquito number, of their specific structure, seasonal dynamics and in penetration of the ecotone and adjacent biotopes. For the hygrophilous mosquitos the microclimatic conditions and the character of vegetation providing shelter in the day time are very important; these elements, as found in the studies, are different in the alder wood, meadow and the ecotone. In the system alder wood – meadow,

the ecotone is between the moist biotope – most suitable for the living and hatching of mosquitos – and the biotope with highly variable abiotic conditions, frequently unfavourable for the mosquitos. In such conditions the ecotone is a place of frequent change of abiotic environmental influences. Therefore, the ecotone is colonized by the eurytopic mosquito species well surviving the habitat variability.

These studies on the behaviour of mosquitos in the ecotone, similarly as the previous ones, show that the ecotone is the zone of intensified penetration and mosquito flights. In the ecotone only a small number of mosquitos seek shelter in the vegetation layer, and as the environmental conditions become worse this mosquito fauna become less numerous or disappear completely. Then the ecotone becomes exclusively the zone of flight of mosquitos between the alder wood and the meadow, and in some conditions it becomes the line of mosquito occurrence.

The effect of environmental conditions on the mosquitos in the ecotone is modified by influences of biotic type. And so, e.g., the relative mosquito activity depends on both the existing climatic conditions, and on the mosquito abundance.

Together with the decrease of the mosquito number their activity increases, and this phenomenon has been observed in all three examined biotopes. This allows to maintain for some time a certain level of mosquito density in the habitat, despite their decreasing number. This phenomenon is frequently observed in biotopes of ecotone type. This increase of mosquito activity together with the worse than in, e.g., alder wood, possibilities of being sheltered in the poorly developed vegetation are responsible for the position of mosquitos as an abundant potential prey. But this happens not only in the instance of mosquitos. Arnoldi (1957) says that several animal species react to the ecotone conditions by a change of activity, frequently by its growth, which creates extremely good food conditions for the predators.

For spiders the ecotone is a fully valuable habitat allowing many species to maintain large populations. We deal there with three ecological types of species: so-called “ecotone”, “forest” and “meadow” species, for which the ecological optimum is in one of the three examined biotopes. The “ecotone” species have a broad ecological amplitude as regards various biotic and abiotic factors, and are more tolerant to such factors as the vegetation type (with its proper structure), air humidity, insolation, etc. The conditions in the ecotone are very good for them and they can occur there in great densities. Such species is, e.g., *Linyphia triangularis*, known for its occurrence in great populations in various forest biotopes with different microclimatic conditions and different herb and undergrowth vegetation in various regions of temperate climate.

Numerous occurrence in the ecotone may be also the result of competition with other species colonizing the meadow or forest.

Typical "forest" species, for which in this arrangement of biotopes, the forest is the most suitable one (e.g. *Meta segmentata*, *Floronia bucculenta*, *Tetragnatha montana*), and also "meadow" species (e.g. *Araneus quadratus* or *Xysticus bifasciatus*), for which the best life conditions are on the meadow — colonize the ecotone somehow "forced" by their own, spreading population, very abundant in the most suitable biotope. For these species, the conditions in the ecotone, although within their range of ecological tolerance, are not the most attractive ones but only sufficient.

In both these instances of inter- and intra-specific competition the ecotone may play the part of an "emergency brake", an additional zone allowing to live for the greater number of individuals. It may protect the ecologically weaker species against local disappearance of their population and provide living conditions for them. An additional argument in favour of the ecotone as a habitat — refuge for ecologically different groups of species — is its food abundance, frequently pointed out in different zoological papers. Thanks to this the intra and inter-specific competition for food becomes weaker and allows the formation of large and undestructable populations of invertebrate predators in the ecotone.

6. RESULTS

The studies allowed to find several phenomena and regularities:

a. The examined ecotone has a different species composition, and different abundance of species forming plant and animal communities. Other structure of ecotone communities is a result of different conditions in the transition zone as compared with the typical biotopes.

b. Exclusive ecotone species have not been found (as, e.g., in Lowrie 1968), but distinguished are (as confirmed by the results of other ecological investigations) species preferring the ecotone, i.e., species, which living in different typical biotopes (e.g. here in alder wood or mid-forest meadow) have a greater population density in the ecotone. Among the plants overgrowing the examined biotopes — alder wood, meadow and their ecotone — there are first of all *Calamagrostis lanceolata*, and also *Poa trivialis*, *Deschampsia caespitosa*, *Filipendula ulmaria*, among mosquitos — *Aedes vexans*, which is attached the most to the ecotone, but also in some conditions — *A. punctor*, *A. excrucians* and *A. annulipes*, whereas other mosquito species are more numerous in the alder wood, the most suitable biotope for the mosquitos;

among spiders – *Linyphia triangularis*, *Theridion ovatum*, *Araneus marmoreus*, *A. diadematus*, *Dolomedes fimbriatus* and *Tetragnatha extensa*.

Apart from the obviously “ecotone” species, i.e. the species with the greatest density in the ecotone, there are also species for which the best conditions are in the middle of typical biotopes, but which can also live in the border zones of these biotopes.

c. First group of species: those preferring the ecotone belong as a rule to the eurytopic species. This has been observed for both mosquitos and spiders.

In the ecotone we may also find species, which penetrate there from the typical biotopes where they have the most suitable conditions (second distinguished group of spiders). Some facts show that this takes place when the animal populations increase in number or there is stronger competition with species of similar ecological requirements; then part of the population of these species may in search for free ecological niches move to the ecotone, which provides for them sufficient living and reproduction conditions.

d. The ecological intracommunity compensation is described: a greater share in the spider community of one spider species (*Floronia bucculenta*) at the expense of another with similar ecological requirements (*Linyphia triangularis*) during drought as compared with the less dry year. This phenomenon is typical not only for the ecotone but because of the great variability of environmental conditions in the ecotone as compared with the typical biotopes, it may take place in the ecotone more frequently than inside typical biotopes; it has been observed in another biotope and in a different spider community compared in two years with quite different weather conditions (Łuczak 1963).

e. In autumn (first part of September) the abundance of spiders in the ecotone decreases much quicker than in typical biotopes. It is assumed, that the quickly changing ecological conditions (meteorological factors, withering of plants) affect badly several spider species thus resulting in dying or retreating into the deep parts of typical biotopes by numerous individuals. It is quite possible, that this happens only in the years of drought, but this regularity has also been observed in the previous paper on the ecotone between the mixed forest and alder wood (Dąbrowska-Prot and Łuczak 1968a).

f. The colonisation of habitats by mosquitos, which are not the best biotopes for them is the resultant of three factors: the existing meteorological conditions, number of mosquitos and the range of their flight, which decreases as the season goes by (Dąbrowska-Prot 1960). In spring, at favourable climatic conditions and great number of mosquitos there are many mosquito species in the ecotone. As their number decreases and the climatic conditions

become worse the proportion of mosquitos in the ecotone to those in the deep part of wet alder wood or other biotopes with better conditions, changes. The intensity of penetrating the ecotone by mosquitos decreases. The species the least sensitive to the change of environmental conditions (e.g., *A. vexans*) remain in the ecotone.

g. In the year abundant in mosquitos (favourable weather conditions) the ecotone is the transition zone between the alder wood and meadow, which they also may colonize. But, when their number is small, this ecotone is the boundary of their dispersion. Then, as opposed to the forest and meadow the activity of mosquitos in the ecotone increases and the ecotone becomes the zone of their intensive penetration.

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ANALIZA EKOLOGICZNA EKOTONU LASU OLCHOWEGO I ŁĄKI NA PRZYKŁADZIE DWU GRUP BEZKRĘGOWCÓW

Streszczenie

Celem badań była analiza wpływu ekotonu, który tworzy się na styku lasu i łąki (i którego odrębność mikroklimatyczną i fitosocjologiczną zbadano), na kształtowanie się zespołów komarów leśnych i ich drapieżców — pajaków.

Badania przeprowadzono w latach 1967 i 1968 w środkowej części Puszczy Kampinoskiej. Badany obszar znajduje się na pograniczu jednego z wielkich pasów wydm Puszczy i rozdzielającego je zabagnionego obniżenia.

Strefa przejścia, w której przeprowadzono badania, przebiega pomiędzy olsem (*Carici elongatae-Alnetum*) a śródleśną łąką. Powstała ona przez wycięcie lasu i, jak zwykle w takich wypadkach, jest zjawiskiem bardzo wyraźnym. Wysoka, słabo ugałęziona ściana lasu graniczy tu ze zbiorowiskiem trawiastym.

1. Zróżnicowanie warunków wodnych i troficznych siedliska oraz zróżnicowanie roślinności w strefie przejścia zbadano na transektach liniowych przebiegających od środka lasu ku środkowi łąki. Z wykresów zmienności warunków siedliskowych (Fig. 1) oraz diagramów podobieństwa florystycznego kolejnych zdjęć fitosocjologicznych (Fig. 2) widać, że układają się one w szereg ekologiczny.

2. Badany ols przedstawia zespół roślinny o bardzo homogenicznym charakterze, a łąka to kompleks zbiorowisk roślinnych, tworzących szereg ekologiczny od bagiennej granicy lasu ku suchemu wyniesieniu. Strefę przejścia pomiędzy tymi zbiorowiskami stanowi pas ziołorośli (związek *Filipendulo-Petasition*, rząd *Molinietalia*), typowy dla obrzeżeń lasów olchowych.

3. Z cech strukturalnych badanego olsu charakterystyczne jest zatarcie kępkowej struktury i względne wyrównanie dna lasu, wyraźne odcięcie wysoko umieszczonej warstwy koron drzew od warstw niższych oraz płynne przejście między warstwą krzewów a warstwą runa obejmującego wiele wysokich roślin. Mimo słabego zwarcia koron zacienienie dna lasu jest duże.

4. Struktura bardziej zróżnicowanej florystycznie łąki, choć prostsza, przeważnie dwuwarstwowa, jest zmienna w przestrzeni, podobnie jak i wysokość darni. Charakterystyczna jest duża zwartość niższej warstwy darniowej (15–30 cm wys.) i znaczna ażurowość warstwy pędów kwiatowych (50–100 cm).

5. Struktura zielnej roślinności strefy przejścia jest w pewnym stopniu podobna do struktury łąki, jednak znacznie bardziej zmienna w ciągu sezonu wegetacyjnego. O panujących tu warunkach mikroklimatycznych decyduje głównie silne i długotrwałe ocienienie od południa przez wysoką ścianę lasu, upodabiające je do warunków leśnych.

6. Stwierdzono różnice w mikroklimacie środkowisk typowych — olsu i łąki — oraz ich ekotonu. Szczególnie charakterystyczne były zmiany wilgotności i temperatury zachodzące wieczorem i rano. Stwierdzono wielką zmienność warunków atmosferycznych na łące i względną ich stałość w lesie (Tab. IV, Fig. 4 a). Ekoton pod tym względem był bardziej podobny do lasu niż do łąki.

7. Analizę zespołu komarów przeprowadzono dla dwu lat różniących się znacznie

poziomem liczebności komarów (w 1968 r. komary stanowiły 27% poziomu ilościowego z roku 1967). Stwierdzono różnice w strukturze gatunkowej, liczebności, aktywności oraz rozmieszczeniu przestrzennym komarów w latach 1967 i 1968, wynikające z postępującego wysuszenia się terenu badań. Polegały one głównie na wzroście udziału w zespole komarów gatunków eurytopowych oraz dominanta, zmniejszeniu ogólnej liczby gatunków i wzroście skupiskowego występowania komarów (Tab. V).

8. Przy dużej ogólnej liczebności komarów w terenie, ekoton jest środowiskiem, w którym kształtuje się zespół komarów o charakterystycznej strukturze gatunkowej. Przy małej ogólnej liczebności komarów ekoton staje się głównie strefą penetracji komarów aktywnych; komary nieaktywne nie szukają tu schronienia. Ekoton stanowi wtedy ostrą granicę występowania komarów, ponieważ łąka eliminowana jest całkowicie jako siedlisko komarów (Fig. 6a, b).

9. Dominantem w obu latach na wszystkich stanowiskach wśród komarów aktywnych i nieaktywnych był *Aedes maculatus*. Różnice środowiskowe dotyczyły subdominanta i gatunków akcesorycznych. Gatunkiem typowo ekotonowym był *A. vexans*, występujący na przykład, w wyjątkowo niesprzyjających warunkach w roku 1968, wyłącznie na ekotonie. Gatunki *A. punctator*, *A. excrucians* i *A. annulipes* w około 50% występowały na łące i ekotonie, głównie w tym ostatnim środowisku (Tab. VII).

10. Przy dużej liczebności komarów w terenie, aktywność ich we wszystkich środowiskach była podobna; przy małej – najaktywniejsze były na ekotonie (Fig. 7). Stwierdzono ogólną tendencję polegającą na wzroście aktywności względnej komarów przy spadku ich liczebności w środowisku.

11. W grupie pajaków stwierdzono występowanie szeregu gatunków zwanych w pracy „ekotonowymi”, to znaczy gatunków tworzących w ekotonie populacje bardziej zagęszczone niż w środowiskach typowych (tab. XIII).

12. Wszystkie ekotonowe gatunki pajaków należą do grupy gatunków wspólnych dla badanych środowisk; liczebność ich w przybliżeniu stanowi około 50% (lub więcej) liczebności wszystkich pajaków ekotonu, około 25% liczebności pajaków lasu olchowego i około 10% liczebności pajaków łąki (fig. 8).

13. Rozpatrując zgrupowania pajaków w trzech badanych środowiskach, stwierdzono różnice w strukturze zgrupowań pajaków ekotonu w porównaniu ze zgrupowaniami środowisk typowych polegające na różnym udziale gatunków „ekotonowych” (największy udział), „leśnych” i „łąkowych” (Fig. 8) i największej liczbie gatunków występujących w pełni lata.

14. W suchym roku 1968 stwierdzono mniejszą ogólną liczebność pajaków we wszystkich badanych środowiskach (Tab. XII), przy zachowaniu podobnej jak w roku 1967 struktury dominacyjnej w zgrupowaniach; pająki „ekotonowe” należały w obu latach do tych samych gatunków.

15. W aspekcie sezonowym w pierwszej połowie września stwierdzono w ekotonie zmniejszenie się liczebności szeregu gatunków pajaków, drastyczniejsze i szybsze niż w środowiskach typowych, wywołane zapewne szybciej pogarszającymi się warunkami mikroklimatycznymi (Fig. 13).

16. Stwierdzono w zespole pajaków ekotonu zjawisko kompensacji ekologicznej, które dało się najlepiej zaobserwować na parze gatunków pajaków o wyraźnie naczodzących na siebie niszach ekologicznych – *Linyphia triangularis* i *Floronia buc-*

culenta; gatunek leśny *F. bucculenta* zwiększył w 1968 r. swój udział w zespole pająków w warunkach, gdy gatunek ekotonowy – a zarazem jeden z głównych dominantów lasu olchowego i ekotonu – *L. triangularis* zmniejszyła swą liczebność w środowisku i udział w zespole pająków na skutek zmiany warunków pogodowych (susza i duże nasłonecznienie, Tab. XIV).

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