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THE EFFECT OF SHRUB LAYER ON THE OCCURRENCE OF THE *ICHNEUMONIDAE (HYMENOPTERA)* IN PINE STANDS ON DIFFERENT SITES

ABSTRACT

A total of 12.000 *Ichneumonidae* representing about 680 species were caught in three layers of pine stands on different sites. The structure of ichneumonid communities was determined by the stand layer and site conditions, the effect of the shrub layer being insignificant. 30% of the individuals in the pine canopy were parasites of pine *Microlepidoptera* (dominant: *Diadegma eucerophaga)*. 4% parazitized pine *Macrolepidoptera* and *Diprionidae*, 8% attacked predatory insects and spiders. The effect of the shrub layer was analysed for *Cratichneumon nigritarius, C. fabricator, C. culex, Pleolophus basizonus, Scambus sagax, Diadegma eucerophaga*, and for nine trophic guilds. The oak shrub layer had a positive effect on polyphagous species. This effect was intensified with increasing richness of the site.

INTRODUCTION

The purpose of the study was to analyse the effect of the deciduous shrub layer (oak and beech) on the structure of *Ichneumonidae* communities and on the number and proportions of more important *Ichneumonidae* species paraziting insect pests. The study was carried out in three layers of pine stands located on different sites. An attempt was made to answer the question whether the shrub layer on poor sites of coniferous forests has a positive effect on the occurrence of parasitic insects *(Ichneumonidae)*, which is of great importance to forest management.

Larval *Ichneumonidae* are parasites of various insects and spiders *(Aranei)*. Therefore, they belong to the system of factors controlling fluctuations in the number of insects in forest ecosystems. Prophylactic methods (biological pest control in forests) recommend the introduction of shrub layer into pine stands on the sites of coniferous forests. It is expected to enrich the species composition and numbers of polyphagous parasites infesting plant pests. This may be possible due to an increase in food supply for the phytophages that are main, intermediate or facultative hosts of parasites with complex trophic relationships. In addition, honeydew secreted by aphids and hemolymph of phytophages inhabiting the shrub layer are sources of food for adult parasites. The abundance of such food stimulates the activity and fecundity of parasites, as well as their longevity, which is of particular importance to polyphages, their development being little synchronized with host development [14].

These considerations of favourable effects of the shrub layer are rather theoretical as there are very few comprehensive field studies supporting them. Many authors studying plant-phytophage-parasite systems do not pay sufficient attention to the type of the site on which forests grow, and they extrapolate the results obtained in forests growing on fertile sites to those on poor sites where the effect of the shrub layer on parasites need not be the same. The possible difference may result from the fact that particular parasitic species the hosts of which live in the shrub layer can also depend on other layers of the vegetation, for instance, on the herb layer, the latter being usually more diversified on richer sites. Also the physiological condition of young trees forming the shrub layer is of great importance to the hosts of parasites, and it depends on soil fertility and water table. It should also be remembered that the shrub layer influences microclimate; overshadowing the soil, it reduces the herb layer with associated insect communities, and it has also an effect on soil moisture and soil processes. All these factors have either a direct or indirect effect on the occurrence of parasites.

It has frequently been stressed that multispecies stands with a rich herb layer (i.e. growing on fertile sites) are characterized by more diversified parasite communities, as compared with pine stands without the shrub layer [9, 12, 33, 47]. Hence, it is concluded that the introduction of a deciduous shrub layer into pine stands on the sites of coniferous forests should increase their natural resistance to insect pests [11, 19, 43, 53].

Only some authors dealing with this problem presented figures indicating that pine stands without the shrub layer on poor sites are more exposed to insect pests, and the rate of pests infestation by parasites rises with increasing diversity and richness of plant cover on the forest floor, the latter being closely related to increasing site fertility. Eidmann [9] and Schwenke [45] have found such relationships for parasites emerging from pupae of *Bupalus piniarius*, and Steiner [48] for parasites infesting *B. piniarius* eggs. Nunberg [28] pointed out that the proportions of egg parasites and parasites emerging from pupae of *Panolis flammea* increased with species diversity of stands (with site fertility).

Szyszko [50] pointed out that on the sites of poor coniferous forests the density and the numbers of *Carabidae* species were lower in pine stands with the shrub layer than in pine stands without this layer. Therefore, the shrub layer under these conditions may not stimulate beneficial insects.

Few papers deal with the ecology of the *Ichneumonidae*, and only some of them list the members of ichneumonid communities occurring in definite forest ecosystems [2, 17, 30—33, 41].

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Grateful acknowledgements are extended to Mr. G. Heinrich (Dryden, Maine, USA), Mr. E. Hinz (Einbeck, FRG), and Dr. K. Horstmann (Würzburg, FRG) for identifying some *Ichneumonidae* to species. Dr. E. Kierych (Institute of Zoology PAS, Warsaw) provided comparable materials of *Ichneumonidae*, and Dr. A. Kolk (Institute of Forest Research, Warsaw) supplied materials of *Ichneumonidae* reared in the laboratory from *Exoteleia dodecella* and *Ocnerostoma piniarella*.

The paper is based on materials for Ph. D. thesis prepared at the Institute of Forest and Wood Protection, Warsaw Agricultural University, under the direction of Professor Andrzej Szujecki.

STUDY AREA, METHODS AND MATERIALS

The study was carried out in pine stands 40—60 years old, a few hectars in area, with and without the shrub layer, growing on different sites and located in distant regions:

Gościeradów (near Kraśnik) — the site of deciduous forest, DF, *Tilio-Carpinetum* Tracz.,
— the site of coniferous forest, CF(1), *Peucedano-Pinetum* Mat.,

Smolniki (near Iława) — the site of mixed coniferous-deciduous forest, MCF, *Fago-Quercetum* Tx.,
— the site of coniferous forest, CF(2), *Leucobryo-Pinetum* Mat.,

Kromnów (Kampinos Forest, near Warsaw) — the site of coniferous forest, CF(3), *Peucedano-Pinetum* Mat.

The only difference among plots within one site was the presence or absence of the shrub layer, with associated consequences such as, for instance, reduced herb layer in the presence of the shrub layer. Only in the stand without the shrub layer at Kromnów (CF) single birches were present. The main study was conducted in 24 plots, including three for each stand. Supplementary materials were collected at Kromnów, where there were only two plots. Soil and plant communities were analysed by respective specialists. Characteristics of site conditions and vegetation of the stands under study have been tabulated by Szyszko [50] [1].

Several methods of sampling flying insects are known. In this paper ichneumonids were caught by means of yellow cups holding liquid and by the sweeping method.

Coloured cups with liquid for catching flying insects belong to the short-distance attracting traps. The catchability of insects depends on their activity and the force of attraction of the traps of a definite colour. In this study yellow traps were used as it has been shown for crop fields [39] and seashore habitats [15] that the traps of this colour attracted 3—4 times as many *Ichneumonidae* as the traps of other colours. At Gościeradów and Smolniki plastic yellow cups were used of 18.5 cm upper diameter, 7.5 cm lower diameter, and 8 cm deep.

At Kromnów plastic yellow boxes were used 12.5 cm deep, with an outlet of 8 × 8 cm. They contained water and 5% glycol (to preserve animals) with liquid soap FF (to lower the surface tension of water); the trapped insects could sink readily in it. The traps (cups and boxes) were placed at three levels: a) in the herb layer, b) at one-sixth of the stand height, and c) in the canopy (Fig. 1). There were 9 traps in each plot, including three at each level and three at each height. At level *a* the traps were usually placed on the ground surface, at level *b* they hung so that they were conspicuous, and at level *c* they hung in external parts of pine crowns. The traps were visited every 7 or 14 days, all ichneumonids being removed. The material obtained at a definite level during one survey of the plot was considered as a sample.

The sweeping method is frequently used to estimate the number of insects, particularly, in crop fields. In forest habitats this method was used by Ozols [30, 32] to determine the number of *Ichneumonidae*. In the present study sweeping was regarded as the supplementary method. A sweep net of 34 cm in diameter was used to sample insects in the herb and shrub layers of each stand. Sweeping was done along parallel lines over the stand. Single sweeps were taken every three steps. The number of individuals taken in 150 sweeps in the herb layer or in 50 sweeps in the shrub layer per stand per day was considered as a sample.

A total of 1.040 samples was taken by the trapping method and 216 by the sweeping method.

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[1] The abbreviations used in this paper correspond to the following abbreviations used by Szyszko: DF = FDF, MCF = FMCF, and CF = FCF.

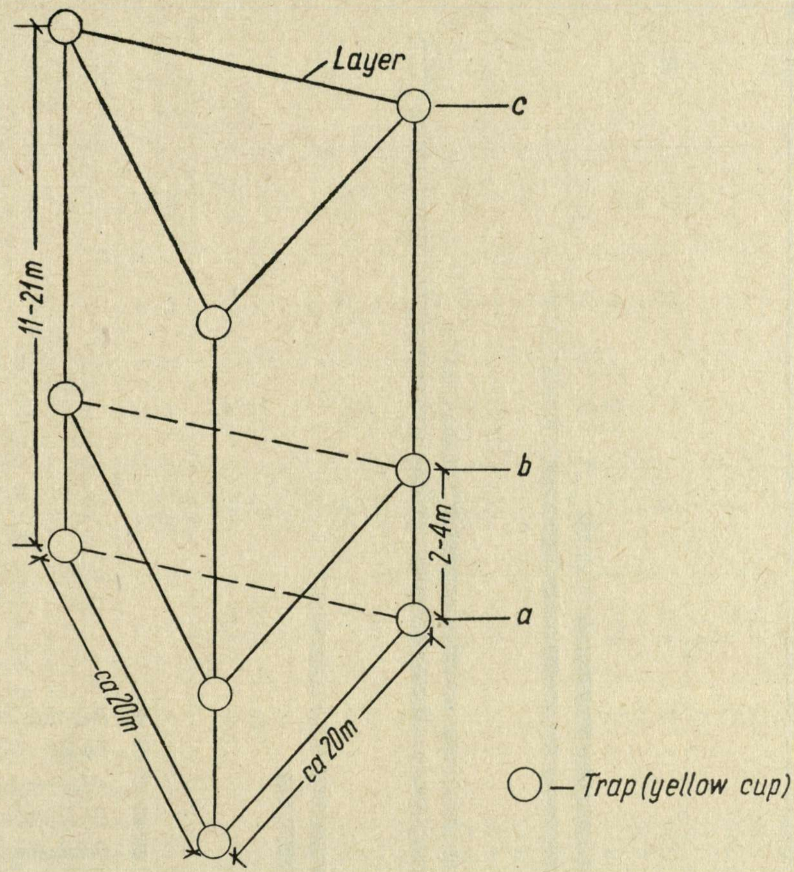


Fig. 1. The distribution of traps in a plot: a — herb layer, b — 1/6 of the stand height, c — pine canopy.

The field observations of ichneumonids at Gościeradów and Smolniki were conducted for about five months from the end of May to the end of October, in 1971 and 1972, respectively, and at Kromnów from 5 June to 12 September, 1972.

The pests of pine were sampled at Gościeradów and Smolniki in the autumn, at the end of October. In each of the plots there were 2—4 subplots under the canopy, and 68 subplots in total. The litter was searched to mineral soil to estimate the density of pests (Fig. 2).

As much as 12.203 ichneumonids were caught by the trapping and sweeping methods in all the plots together (Tab. 1). 95% of the material collected comprised 535 species. The whole material probably consisted of 680 species. From larval lepidopterans and cocoons of *Diprionidae* collected in the autumn, 34 individuals of nine ichneumonid species were raised in the laboratory. A relatively small number of

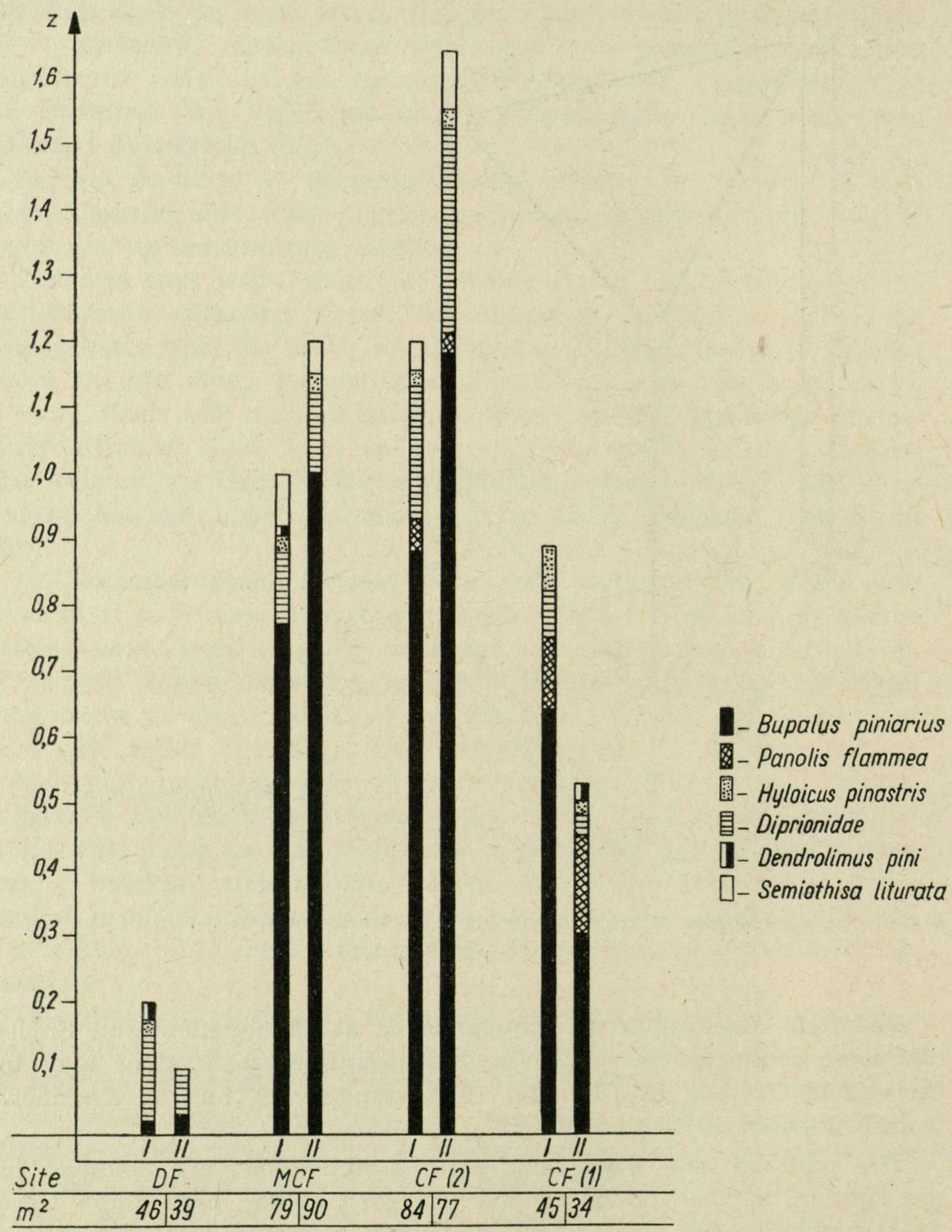


Fig. 2. Average number of primary pine pests per 1 m² of subcanopy surface area łz) in stands with the shrub layer łI) and without (II), on different sites.

Ichneumonidae was not identified but they included many species represented by single individuals. So, the diagram (Fig. 3) showing the number of ichneumonid species caught at particular levels of the stands provides only an approximate picture of the species composition.

Table 1. Total number of *Ichneumonidae* caught (n), average number of individuals caught per day per trap (n') and average number of individuals caught per sweep (n'') at three levels (a — herb layer, b — 1/6 of the stand height, c — pine canopy), and average numbers of individuals for the whole pine stands (N') with the shrub layer (I) and without (II), on different sites

Location	Forest site	Shrub layer	Level	Yellow cups				Sweep-net				Total
				I		II		I		II.		
				n	n'	n	n'	n	n''	n	n''	
1	2	3	4	5	6	7	8	9	10	11	12	13
Gościeradów	DF	Oak-Horn.	a	309	0,23	289	0,24	717	0,18	461	0,10	
			b	150	0,11	148	0,12	59	0,05	—	—	
			c	124	0,16	68	0,16	—	—	—	—	
			N'	583	0,17	505	0,17	776		461		2 325
	CF (1)	Oak	a	895	0,82	1 366	1,15	131	0,04	171	0,05	
			b	646	0,54	488	0,41	337	0,32	—	—	
			c	204	0,20	348	0,33	—	—	—	—	
			N'	1 745	0,52	2 202	0,63	468		171		4 586
Smolniki	MCF	Oak	a	122	0,22	321	0,28	249	0,21	188	0,15	
			b	278	0,22	327	0,23	40	0,12	—	—	
			c	556	0,42	474	0,33	—	—	—	—	
			N'	956	0,29	1 122	0,28	289		188		2 555
	CF (2)	Beech	a	187	0,26	198	0,21	37	0,04	55	0,04	
			b	144	0,11	201	0,17	6	0,02	—	—	
			c	496	0,36	767	0,55	—	—	—	—	
			N'	827	0,24	1 166	0,31	43		55		2 091
Kromnów	CF (3)	Oak	a	65	0,27	172	0,34	—	—	—	—	
			b	53	0,10	92	0,14	—	—	—	—	
			c	92	0,31	172	0,43	—	—	—	—	
			N'	210	0,23	436	0,30					646
Total number				4 321		5 431		1 576		875		12 203

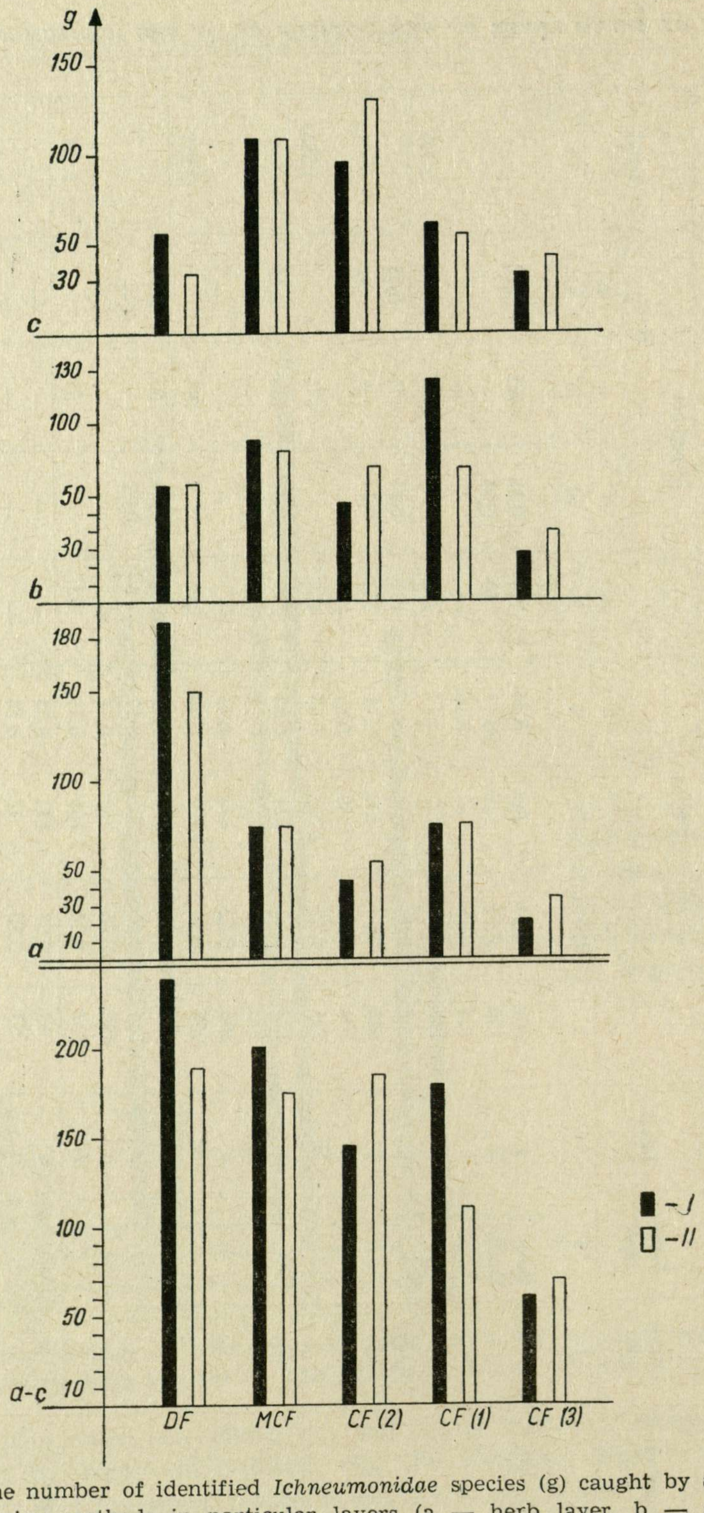


Fig. 3. The number of identified *Ichneumonidae* species (g) caught by the trapping and sweeping methods in particular layers (a — herb layer, b — shrub layer, c — pine canopy) and in the whole stands (a-c) with the shrub layer (I) and without (II), on different sites.

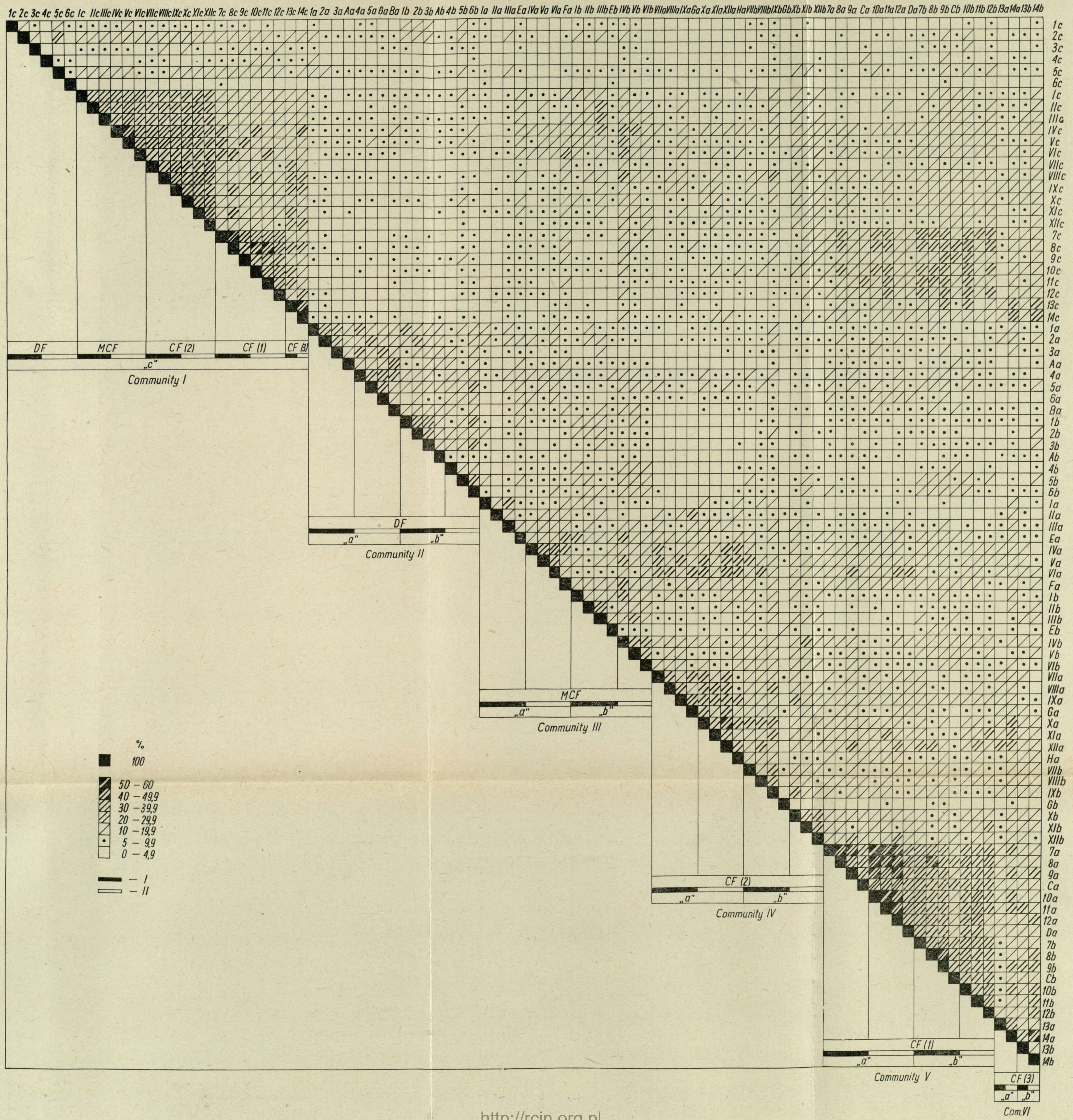


Fig. 5. The indices of species similarity (*Ja*) for *Ichneumonidae* in particular layers (a — herb layer, b — shrub layer, c — pine canopy) of pine stands with the shrub layer (I) and without (II), on different sites. Based on the materials collected by the trapping method (plots 1—14 and I—XII) and by the sweeping method (stands A—H).

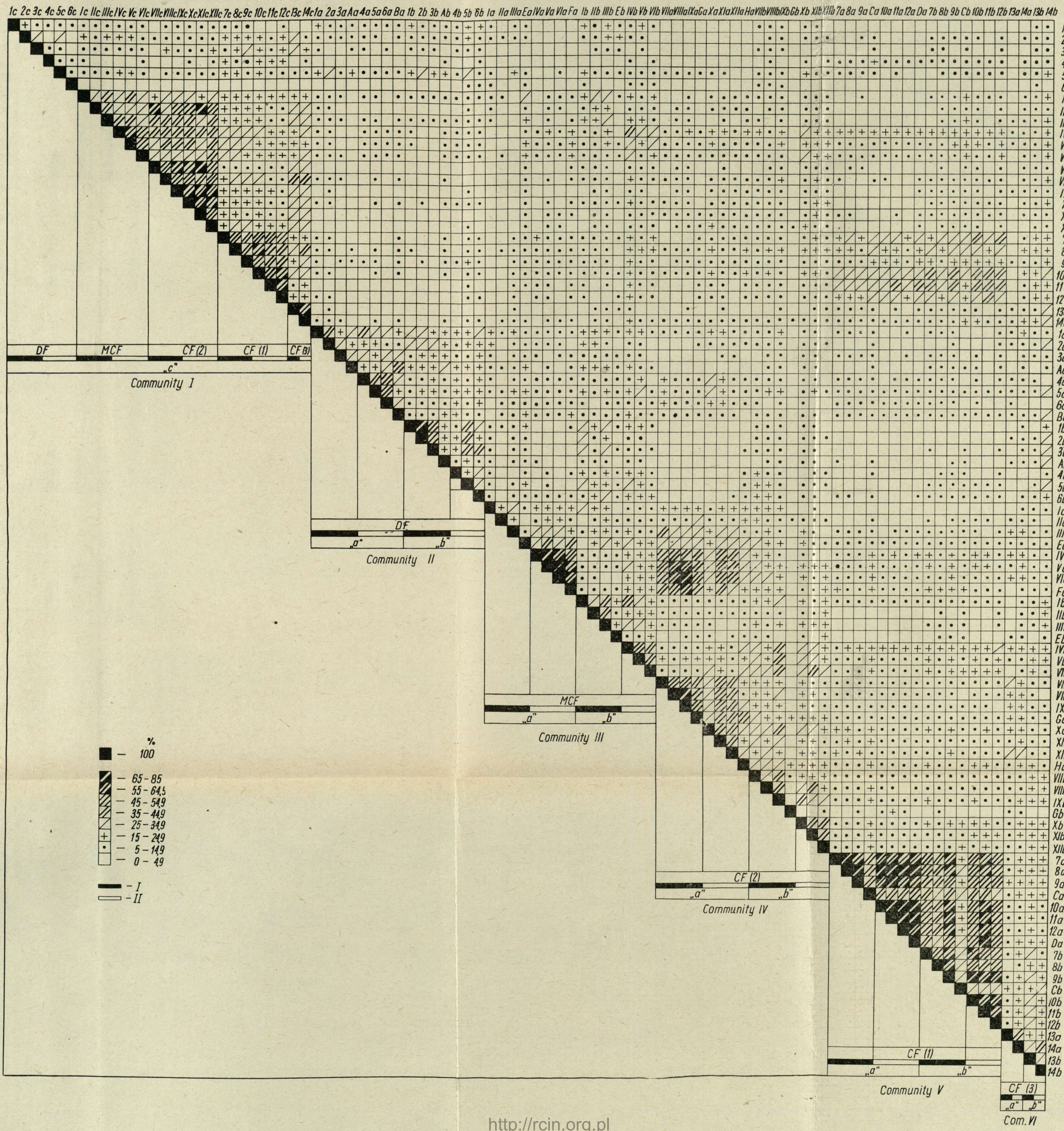


Fig. 6. The indices of domination similarity *(Re)* for *Ichneumonidae* in particular layers (a — herb layer, b — shrub layer, c — pine canopy) of pine stands with thet shrub layer (I) and without (II), on different sites. Based on the materials collected by the trapping method (plots 1—14 and I—XII) and by the sweeping method (stands A—H).

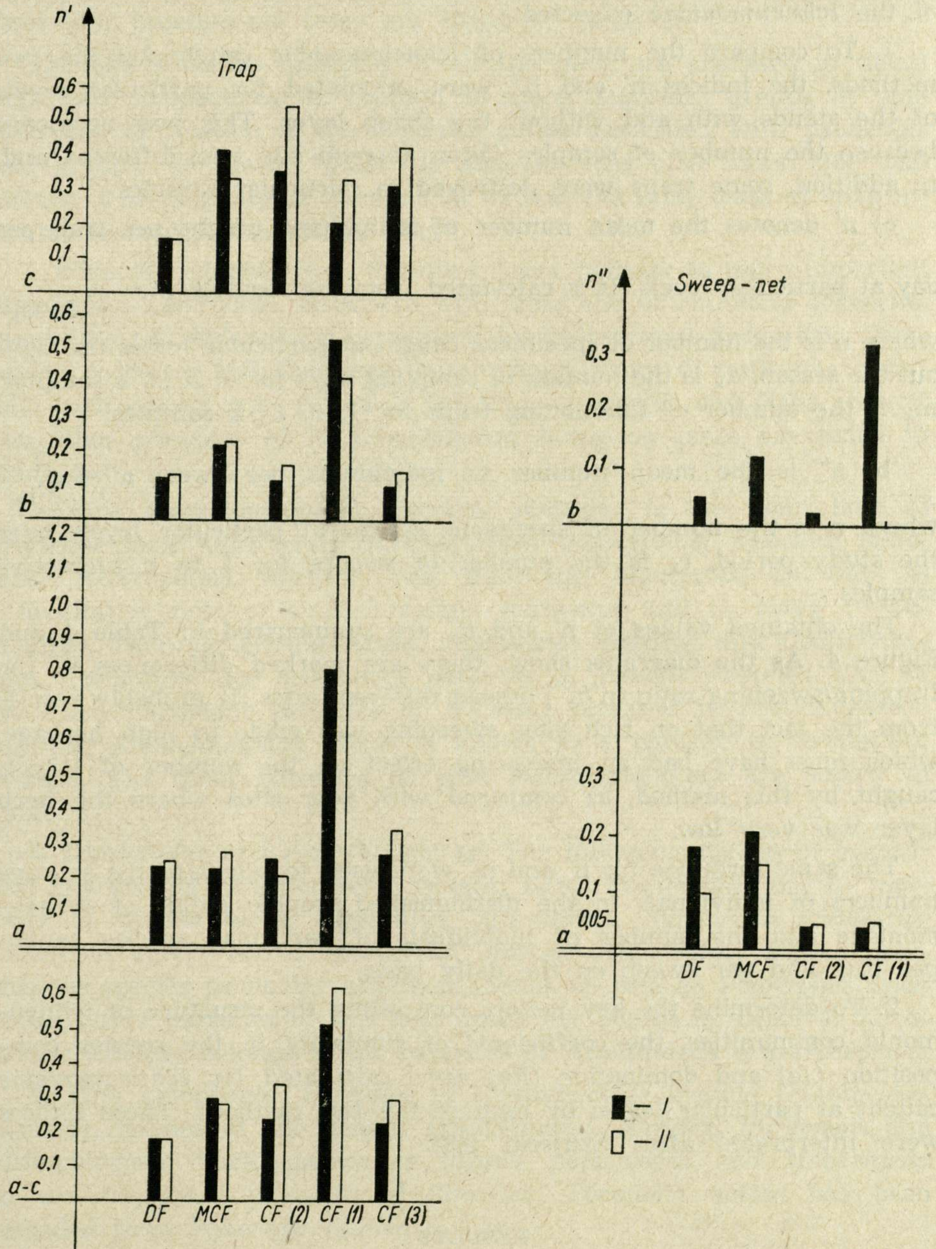


Fig. 4. Comparison of the average number of *Ichneumonidae* caught per day per trap (n') or per sweep (n") in particular layers (a — herb layer, b — shrub layer, c — pine canopy) and in the whole stands (a-c) with the shrub layer (I) and without (II), on different sites.

Some indices were used for quantitative and qualitative analysis of the *Ichneumonidae* collected:

1. To compare the numbers of *Ichneumonidae* caught by the two methods, the indices n′ and n″ were calculated for particular levels of the stands with and without the shrub layer. This was necessary because the number of samples taken at each site was different and, in addition, some traps were destroyed in particular samples.

a) n′ denotes the mean number of individuals caught per trap per day at particular levels. It is calculated from the formula $n' = \frac{n}{\sum d_k \cdot m_k}$, where n is the number of specimens caught at particular levels throughout the season, d_k is the number of sampling days for 1, 2, ..., k samples, m_k is the number of functioning traps for 1, 2, ..., k samples.

b) n″ is the mean number of individuals per sweep $n'' = \frac{n}{\sum c_k}$, where n is the number of specimens caught at particular levels over the study period, c_k is the number of sweeps for 1 to k successive samples.

The obtained values of n′ and n″ are summarized in Table 1 and Figure 4. As the diagrams show, there are marked differences in the trapping/sweeping ratio (n′/n″) among different sites. It probably results from the fact that on rich sites sweeping was made in high herbage, which must have had an increasing effect on the number of insects caught by this method, as compared with poor sites where the herb layer was very low.

The same formulae for n′ and n″ were used to calculate the average numbers of individuals in the distinguished trophic guilds of *Ichneumonidae* and the number of individuals of particular species caught per trap and per sweep on the daily basis.

2. To determine the key factors controlling the structure of ichneumonid communities, the coefficients of similarity in the species composition *(Ja)* and domination *(Re)* were calculated for *Ichneumonidae* caught at particular levels by each of the two methods. These indices were interpreted after Szujecki [49].

RESULTS

HOSTS OF THE *ICHNEUMONIDAE* CAUGHT

The data presented in this paper on hosts of the parasites caught were partly obtained from laboratory cultures but mostly from the extensive literature, which is largely quoted in an earlier paper [41]. Here also other papers on hosts were used [1, 3—9, 13, 16, 18, 20—37, 42, 44—48, 51, 52]. The *Ichneumonidae* the hosts of which live on pines and broadleaved trees are listed in Table 2.

The ichneumonids collected in all the plots are analysed in detail from two perspectives: in relation to more important groups of pine pests and in relation to ichneumonid guilds associated with particular host groups. The term "guild" is adopted here after Root [38] who defined it as "a group of species that exploit the same class of environmental resources in a similar way".

1. Pine *Microlepidoptera*. *Scambus sagax* belongs to more important parasites of *Tortricidae* associated with pines and of *Exoteleia dodecella*. In addition, *E. dodecella* is parasitized by *Stilbcscopus dodecellae, Campoplex rufinator* and *Diadegma eucerophaga*. From *Ocnerostoma piniarella* such species were raised as *Eriplatys ardeicollis* and *Gelis areator*. The other parasites of *Microlepidoptera* living on pines are listed in Table 2.

2. Pine *Macrolepidoptera*. *Bupalus piniarius* is the main host of *Cratichneumon nigritarius, Barichneumon bilunulatus, Banchus femoralis, Heteropelma calcator*, and *Habronyx biguttatus*, as well as a facultative host of *Cratichneumon fabricator* and *C. culex* (= *annulator*). *Theronia circumflexum, Aphanistes armatus* and *Coelichneumon "comitator"* are specialized parasites of *Panolis flammea*. One of the more important parasites of *Hyloicus pinastris* is *Protichneumon fusorius; Stenichneumon pictus* is known as a parasite of *Semiothisa liturata*. The other parasites of pine *Macrolepidoptera* are shown in Table 2.

3. *Diprionidae* and *Acantholyda* sp. The following species of specialized *Diprionidae* parasites were caught: *Lamachus frutetorum, L. transiens, L. ophthalmicus, Hypsantyx lituratorius, Synomelix scutulatus, Exenterus amictorius, E. adspersus, Aptesis subguttatus;* among polyphagous species particular attention should be paid to *Pleolophus basizonus*. Other parasites of this host group are shown in Table 2. *Xenoschesis fulvipes* belongs to the parasites of *Acantholyda erythrocephala*.

4. Pine xylophages. Parasites of *Cerambycidae* include *Odontocolon ruspator*, species of the genera *Dolichomitus, Xorides, Pyracmon* and *Rhimphoctona*. Such species as *Rhyssa persuasoria* and *Megarhyssa* sp. are important parasites of *Siricidae*. *Poemenia notata* has been recorded from *Phaenops cyanea*.

5. Insects feeding on cones. In the crowns of pines on the CF (1) site many individuals of *Idiogramma euryops* were caught. They are parasites of *Symphyta* of the genus *Xyela*, the larvae of which live in pine cones.

6. *Microlepidoptera* associated with deciduous trees. The captured parasites of *Tortrix viridana* are shown in Table 2. The other *Micro-*

Table 2. Species composition of the *Ichneumonidae* that are potential parasites of insects associated with pines and deciduous trees

Ichneumonidae	Pine phytophages									Deciduous-tree phytophages			
	Microlepidoptera			*Macrolepidoptera*									
	Exoteleia dodecella L.	*Rhyacionia buoliana* Schiff.	*Petrovia resinella* L.	*Bupalus piniarius* L.	*Panolis flammea* Schiff.	*Dendrolimus pini* L.	*Lymantria monacha* L.	*Diprionidae*	Xylophages	*Tortrix viridana* L.	Other *Microlepidoptera*	*Lymantria dispar* L.	Other *Macrolepidoptera*
1	2	3	4	5	6	7	8	9	10	11	12	13	14
Scambus signatus Pfef.								+					
S. calobata Grav.		+	+							+	+		+
S. detritus Holmgr.		+								+			
S. planatus Hartig		+	+							+			
S. sagax Hartig	+	+	+								+		
Gregopimpla inquisitor Scop.		+	+			+	+		+		+	+	+
Dolichomitus spp.									+				
Acropimpla pictipes Grav.										+			
Itoplectis alternans Grav.		+					+	+		+	+		+
I. maculator F.	+	+	+							+	+		+
Ephialtes compuctor L.							+			+	+	+	+
E. quadridentatus Thoms.							+	+		+	+		+
E. rufatus Gmel.						+	+	+		+	+		+
Coccygomimus aquilonia Cress.										+	+		+
C. contempolator Muell.		+					+						+
C. instigator F.		+		+	+	+	+			+		+	+
C. turionellae L.		+	+				+	+		?	+	+	+
Theronia atalantae Poda			+	+		+	+			+		+	+
Poemenia notata Holmgr.									+				
Rhyssa persuasoria L.									+				
Megarhyssa sp.									+				
Phytodietus segmentator Grav.										+	+		
Netelia cristata Thoms.												+	
N. tarsator Thunb.												+	
N. latungula Thoms.												+	
Exenterus amictorius Pnaz.								+					
E. adspersus Hartig								+					
Odontocolon ruspator Fourcr.								+					
Xorides spp.									+				
Gelis areator Grav.				+				+		+	+	+	
G. cinctus Grav.		+											
Stiboscopus dodecellae Obrt., Šed.	+												
Endasys erythrogaster Grav.								+					

1	2	3	4	5	6	7	8	9	10	11	12	13	14
E. rusticus Haberm.								+					
E. brevis Grav.											+		
Bathythrix claviger Taschenb.								+					
Pleolophus basizonus Grav.								+					
P. sericans Grav.								+					
Aptesis abdominator Grav.					+								
A. subguttatus Grav.								+					
Polytribax arrogans Grav.				+	+								+
Agrothereutes adustus Grav.		+						+					
A. abbreviator Grav.											+		+
Pycnocryptus director Thunb.													+
Ischnus porrectorius F.										+	+	+	+
Apophua evanescens Ratz.											+		+
A. bipunctoria Thunb.		+								+	+		
Glypta ceratites Grav.											+		
G. resinanae Hartig		+	+										
Lissonota variabilis Holmgr.			?								+		
L. buolianae Holmgr.		+											
L. errabunda Holmgr.		+										+	
L. piceator Thunb.					+							+	
Exetastes illusor Grav.				+									
Banchus monileatus Grav.					+								
B. femoralis Thoms.					+							+	
Rhorus substitutor Thunb.								+					
Phaestus anomalus Brischke											+		
Lamachus frutetorum Hartig								+					
L. ophthalmicus Holmgr.								+					
L. transiens Ratz.								+					
Synomelix scutulatus Hartig								+					
Hypsantyx lituratorius L.								+					
Sinophorus crassifemur Thoms.		+											
Campoplex mutabilis Holmgr.		+								+	+	+	+
C. rufinator Aub.	+										+		
C. difformis Gmel		+					+			+	+	+	
Casinaria nigripes Grav.						+							+
C. rufimana Grav.													+
C. ischnogaster Thoms.												+	+
C. albipalpis Grav.													+
Rhimphoctoma sp.									+				
Leptocampoplex cremastoides Holmgr.	+												
Pyracmon fumipennis Zett.									+				
P. melanurus Holmgr.									+				
Campoletis zonata Grav.													+
Dusona oxycanthea Boie					+								+
D. foersteri Roman											+	+	
Tranosema aerenicola Thoms.											+		
Diadegma eucerophaga Horstm.	+												
D. fenestralis Gmel.										+			
Hyposoter clausus Brischke													+
Olesicampe macellator Thunb.								+					

1	2	3	4	5	6	7	8	9	10	11	12	13	14
Pristomerus orbitalis Holmgr.	+	+				+					+	+	
Enicospilus ramidulus L.					+								+
Triclistus podagricus Grav.											+		
T. laevigatus Ratz.											+		
Exochus flavomarginatus Holmgr.											+		
E. decoratus Holmgr.											+		
Habronyx nigricornis Wesm.										+	+		
H. biguttatum Grav.				+	+	+							
Aphanistes armatus Wesm.				+	+								+
Agrypon flaveolatum Grav.											+		+
Theronia circumflexum L.					+	+							+
Heteropelma calcator Wesm.				+	+								+
H. amictum F.													+
Coelichneumon "comitator" L.				+	+								+
C. fuscipes Gmel.					+								
Stenichneumon lineator F.					+						+		
S. pictus Gmel.												+	
S. culpator Schrank													+
Aoplus ochropis Gmel.													+
Ichneumon deliratorius Grav.													+
Cratichneumon sicarius Grav.				+									+
C. luteiventris Grav.					+								
C. corruscator L.					+								+
C. versator Thunb.				+	+								
C. varipes Grav.											+		
C. culex Muell.				+	+								+
C. nigritarius Grav.				+	+		+						+
C. fabricator F.				+	+							+	+
C. rufifrons Grav.													+
C. disimilis Grav.				+									
Eupalamus oscillator Wesm.													+
Barichneumon dumeticola Grav.					+								+
B. locutor Thunb.				+									+
B. praeceptor Thunb.				+									
B. derogator Wesm.					+								
B. bilunulatus Grav.				+	+								+
Ctenichneumon rubroator Ratz.					+								+
Hepiopelmus variegatus Panz.				+									+
Platylabus conthurnatus Grav.				+									
Pristiceros serrarius Grav.													+
Hypomecus quadriannulatus Grav.													+
Stenodontus marginellus Grav.												+	
Phaeogenes vagus Berth.		+											
Ph. spiniger Grav.											+		
Ph. invisor Thunb.										+	+		
Ph. impiger Wesm.													

lepidoptera of this group consist of 14 species, including *Archips rosana* and *Choristoneura sorbiana*.

7. *Macrolepidoptera* associated with deciduous trees. Parasites of *Lymantria dispar* are listed in Table 2. The other macrolepidopteran hosts of the *Ichneumonidae* caught involve 27 species, including *Dasychira pudibunda, Malacosoma neustrium, Operophthera brumata,* and *Phalera bucephala.*

8. Parasitic insects. *Lysibia nana* parasitize, among others, *Apanteles* spp.; *Tachinidae* are attacked by species of the genus *Phygadeuon.* More than 10 species of this genus were caught, including *Ph. exiguus, Ph. vexator* and *Ph. trichops. Mastrus inimicus* has been recorded as a hyperparasite of *Diprionidae,* parasites of *Exenterus* spp. and other *Ichneumonidae. M. castaneus* parasitize *Banchus* sp., *Exenterus* sp. (*Ichneumonidae)* and *Meteorus (Braconidae).* Among the hosts of species of the genus *Theroscopus,* the most common are *Ichneumonidae* and *Braconidae; Th. esenbecki* parasitize *Banchus* sp., while *Th. pedestris* is a parasite of *Meteorus* spp. The genus *Gelis* is represented in Poland by several species, the biology of which is very diversified. They may be parasites or hyperparasites; their larvae can also live in spider egg sacks. *Gelis areator* is an example of such polyphages. Such polyphagous species as *Pleolophus basizonus* and *Politribax arrogans* were also raised from cocoons of *Banchus* sp. *Mesochorinae* are exclusively hyperparasites infesting *Tachinidae, Braconidae* and *Ichneumonidae.* Such species as *Astiphromma strenuum, Mesochorus fulgurans* and *M. longicauda* are known hyperparasites of *Diprionidae. M. silvarum* and *M. politus* are hyperparasites of *Tortrix viridana* and *Bupalus piniarius,* respectively.

9. Predatory insects. *Ichneumonidae* are parasites of predatory insects of several orders. Predatory *Syrphidae* are parasitized by species of such genera as *Homotropus, Enizeum, Syrphophilus, Diplazon, Promethes, Sussaba (Diplazontinae),* as well as by *Bathythrix pellucidator, Phygadeudon ovatus* and *Ethelurgus sodalis.* Among the parasites of *Chrysopidae* there were caught *Dichrogaster aestivalis* and *D. schaffneri; Hemerobiidae* were parasitized by *Charitopes chrysopae; Rhaphidiidae* were attacked by species of the genus *Nemeritis. Sphecidae* are hosts of *Perithous mediator* and *Aritranis* spp.

10. *Aranei.* The species of *Ichneumonidae* caught that are associated with spiders infest mainly their egg cocoons. This type of parasitism is developed in *Ephialtinae* and *Galinae. Ephialtinae* were represented by species of the genera *Tromatobia, Zaglyptus, Clistopyga, Acrolyta, Polysphincta,* and *Zatypoda; Gelinae* were represented by the genera *Trychosis, Acrolyta* and *Gelis.*

11. *Diptera* living in fungi. *Mycetophilidae* are hosts of the majority of species of the subfamily *Microleptinae*, genera *Proclitus*, *Plectiscidea*, *Apereliptus*, *Eusterinx* and *Megastylus*.

The hosts of many *Ichneumonidae* recorded in this study are not known. This is, for instance, *Macrus parvulus*, abundant in pine crowns.

COMMUNITIES OF *ICHNEUMONIDAE*

Numbers and species composition of *Ichneumonidae* occurring at particular levels of the stands under study were controlled by a number of interrelated factors. The occurrence of parasites and their hosts could be determined by the richness of plant cover on the forest floor (including introduced deciduous trees in the shrub layer), geographical location and, in this relation, climate and weather conditions. To find the key factors controlling the structure of ichneumonid communities, the similarity coefficients of species composition *(Ja)* and domination *(Re)* were calculated for ichneumonids collected at particular levels of the stands under study. The results are presented in the form of Czekanowski's diagrams (Figs 5 and 6), in which the stands are arranged in such a way that the successive levels in one stand are most similar to corresponding levels of another stand (their coefficients have the highest values). This is the relatively most convenient arrangement of the stands to indicate the key factors controlling ichneumonid communities in them. Six distinct communities can be identified from Czekanowski's diagrams. Site conditions with the associated plant cover on the forest floor were considered as key factors controlling ichneumonid communities in lower layers. The very distinct community in the canopy of all the stands (community I) was only slightly influenced by site conditions and plant cover of the forest floor. The only exception was the stand on the CF(1) site where the ichneumonid community in the canopy was influenced by that in lower layers. But it was due to the fact that in this stand there was an outbreak of some ichneumonid species associated with the herb layer; as the stand was low (about 13 m high), they penetrated also the canopy. A high similarity between ichneumonid communities in the herb and shrub layers on the MCF and CF sites in Smolniki can be explained by relatively small differences in site conditions and by the fact that the observations were made in the same year.

In addition, Czekanowski's diagrams indicate that the presence of deciduous trees (oak and beech) in the shrub layer which covered from 10 to 50% of the area (the beech shrub layer on the CF(2) site covered even 70%) had no remarkable effect on the structure of ichneumonid communities on the CF site, as compared with the plots without the shrub layer. It was observed, however, that the shrub layer on the

DF, MCF and CF(1) sites modified to some degree the occurrence of *Ichneumonidae* in lower layers of the stands (mainly the proportions of some species in the community). It is difficult, however, to estimate the effect of the shrub layer on ichneumonid communities because of a rather large variability in *Ichneumonidae* occurrence on particular plots of the same stand.

It has been found that the effect of shrub layer on the numbers and species composition of ichneumonid communities in the pine stands under study was not sufficiently pronounced to distinguish them from ichneumonid communities occurring in pine stands without the shrub layer on the same sites.

Community I consisted of *Ichneumonidae* inhabiting the pine canopy of all the sites at Gościeradów, Smolniki and Kromnów. In all the plots 3.301 specimens representing more than 264 species were caught.

Because of differences in the site and geographical conditions as well as in weather conditions from year to year, there were some differences in the abundance of species characteristic of this layer, and associated with hosts living there.

Community I was dominated by *Diadegma eucerophaga* (17.0%). The following species accounted for 1—4.3% of the total number of *Ichneumonidae* caught in the canopy: *Ichneumon subquadratus*, (4.3%), *Scambus sagax* (4.0%), *Trychosis legator* (3.5%), *Macrus parvulus*, *Gelis areator*, *Lissonota variabilis*, *Idiogramma euryops*, *Tersilochus* sp., *Adelognathus puncticollis*, *Phaeogenes vagus*, *Nemeritis caudatula*, *Eriplatys ardeicollis*, *Clistopyga canadensis* and *Campoplex rufinator;* the proportions of the other species were considerably lower than 1%.

Diadegma eucerophaga, a parasite of *Exoteleia dodecella* was closely associated with the canopy and it did not occur in other layers. Its proportions in the plots at Smolniki and Kromnów varied from 10 to 45% of all individuals caught in the canopy, while at Gościeradów it was not recorded. *S. sagax*, a well known parasite of *E. dodecella* and pine *Tortricidae*, was also caught almost exclusively in the canopy of all the stands. *Phaeogenes vagus*, *Glypta resinanae*, *Compoplex mutabilis, and Coccygominus turionellae* are parasites of *Rhyacionia buoliana; Eriplatis ardeicollis* and polyphagous *Gelis areator* have been recorded from *Ocnerostoma piniarella*. Other known but less frequent parasites of *E. dodecella* are *Campoplex rufinator*, *Stiboscopus dodecellae*, *Phaeogenes impiger* and *Leptocampoplex cremastoides*. All the ichneumonid species listed above represented an important guild of parasites infesting microlepidopteran pine pests. In the pine canopy they accounted for about 30% of insects caught in this layer, this figure being probably underestimated as some parasites the hosts of which are unknown could be overlooked (for instance, *Macrus parvulus*).

A different situation was observed in the case of parasites of pine *Macrolepidoptera*. The numbers and species composition of these parasites were poor. They accounted for only a few percentage of the total number of individuals caught in the canopy. The most numerous parasites in this group include *Banchus femoralis*, *Stenichneumon pictus*, *Casinaria nigripes* and *Coccygomimus turionellae*. Among the species caught both in the canopy and in other layers such species should be mentioned as *Enicospilus ramidulus*, *Theronia circumflexum*, *Aphanistes armatus*, *Barichneumon bilunulatus*, *Coelichneumon „comitator"* and *Protichneumon fusorius*.

Specialized ichneumonid parasites of *Diprionidae* were not numerous. Only *Olesicampe macellator* was a little more frequently observed on the CF(1) site. In different plots single individuals were caught of such species as *Scambus signatus*, *Itoplectis alternans*, *Exenterus amictorius*, *Lamachus transiens*, *Synomelix scutulatus*, *Hypsantyx lituratorius*, *Aptesis subquttatus* and *Agrothereutes adustus*. A relatively more abundant polyphagous *Gelis areator* was also a potential parasite of *Diprionidae*.

Idiogramma euryops, a parasite of *Symphyta* (*Xyela* sp.) living in pine cones was caught only at Smolniki where its proportion reached 6% in some plots.

Parasites of predatory insects and spiders were rather abundant as they contributed to about 8% of the total community. Species of the genus *Nemeritis* are known as parasites of *Raphidia*; *Dichrogaster aestivalis* was raised from *Chrysopa*. Spiders were parasitized by *Trychosis legator*, *Clistopyga canadensis* and polyphagous *Gelis areator*.

The effect of the oak shrub layer on the structure of ichneumonid community I (in the canopy) was relatively small, but it can be characterized as stimulating. Only in some exceptional cases it may be suggested that the increased proportions of some species in the canopy were mainly related to the presence of the oak shrub layer in the stand. *Aptesis abdominator*, which is known as a parasite of *Dendrolimus pini*, at Gościeradów occurred almost exclusively in the plots with the shrub layer on the CF(1) site. Also *Campoplex rufinator*, a parasite of *E. dodecella*, tended to be 3—4 times more abundant in the stands with the oak shrub layer on the coniferous forest sites, while the beech shrub layer on the CF(2) site was not so suitable for this species, the number of individuals caught there being lower by half.

Also the effect of the shrub layer on *Macrus parvulus* can be characterized as negative because the number of individuals caught in the plots with the shrub layer on the MCF and CF(2) sites was 4—8 times lower.

Community II on the DF site at Gościeradów. In the pine stands with the oak-hornbeam shrub layer and without the shrub layer 2 133 ichneumonids representing more than 276 species were caught at the two lower levels.

Cratichneumon culex was the most abundant species (8.0%); the following species accounted for 1—4.7%: *Pleolophus basizonus* (4.7%), *Plectiscidea* sp. (2.7%), *Cratichneumon fabricator* (2.6%), *Encrateola laevigata, Phobocampe bicingulata, Coccygomimus aquilonia, Sussaba cognata, Phygadeuon exiguus, Phaeogenes infirmus, Cratichneumon varipes, Mesoleptus* sp., *Ephialtes quadridentatus, Dichrogaster schaffneri,* and *Charitopes chrysopae.*

The ichneumonid community on the DF site was very rich in individuals and species. This was due to a diversified species composition of the herb layer and presence or absence of the shrub layer. Such species as *C. culex, C. fabricator, E. quadridentatus, C. aquilonia,* and *C. varipes* are known parasites of larger *Lepidoptera* associated with deciduous trees. The first two species are also parasites of *Bupalus piniarius,* and *E. quadridentatus* parasitize *Lymantria monacha. P. basizonus* is an important parasite of *Diprionidae.*

Among the species that can attack insect pests, only the number of *C. culex* was 3.5 times higher in the stands with the shrub layer, as compared to those without the shrub layer. The other species, except for *C. aquilonia,* were more numerous in the stands without the shrub layer. Particularly, the proportion of *P. basizonus* was almost ten times higher in the stands without the shrub layer. The proportion of *C. fabricator* was two times higher in such stands.

Among the specialized parasites of insect pests only single individuals were caught, mostly in the stands without the shrub layer. These were, for instance, *Cratichneumon nigritarius* and *Lamachus* sp. This was an effect of the low density of pine pests in the stands.

Community III occurred in the pine stands with the oak shrub layer and without the shrub layer on the MCF site at Smolniki. A total of 1 525 individuals were caught of more than 201 species.

The most abundant species belonged to the genus *Eusterinx* (18%); the following species accounted for 1.5—4.5% of the community: *Cratichneumon varipes* (4.5%), *C. nigritarius* (3.9%), *C. lanius* (3.3%), *Ichneumon subquadratus* (3.0%), *Cratichneumon culex* (2.7%), *Proclitus grandis, Cratichneumon fabricator, Ichneumon gracilentus, Acrolyta distincta, Netelia latungula.*

The recorded species of the genera *Cratichneumon* and *Netelia* attack macrolepidopterans living on deciduous trees. *C. nigritarius* parasitize *Bupalus piniarius* and *Panolis flammea.* Dominant species of the genera *Eusterinx* and *Proclitus* are associated with dipterans living in fungi, and *Acrolyta distincta* live in spider egg cocoons.

In the stands with the shrub layer some polyphagous species were 2—30 times more abundant in the stands without the shrub layer, and their proportions were considerably higher. These were such species as *C. lanius, C. culex, C. fabricator,* and *Netelia latungula.* They are parasites of lepidopterans associated with deciduous trees, so they are likely to find suitable hosts in the shrub layer. Also *Coccygomimus conteplator* occurred only in the stands with the shrub layer, although less abundantly.

Community IV consists of *Ichneumonidae* caught in the lower part of the pine stands with the beech shrub layer and without the shrub layer, on the CF(2) site at Smolniki.

A total of 828 individuals representing more than 149 species were recorded. Dominant species of the genus *Eusterinx* (17.4%) were the same as on the MCF site. Among the species accounting for 1—8% of the community there were *Cratichneumon basizonus* (5.3%), *Proclitus grandis, Cratichneumon varipes, Macrus parvulus, Dialipsis conjuctor, Odontocolon ruspator, Ichneumon subquadratus, Acrolyta distincta,* and *Mesoleius* sp.

About 25% of the total number of *Ichneumonidae* caught were represented by species of *Microleptinae,* which are parasites of dipterans living in fungi. Among the parasites of insect pests, the most abundant were *C. nigritarius, P. basizonus* and *Odontocolon ruspator.* These species were more numerous in the stands without the shrub layer. *Macrus parvulus,* which is rather associated with the canopy, occurred also in lower layers, but more frequently in the stands with the shrub layer. Also *Coelichneumon „comitator"* and *C. fuscipes,* the species attacking *Panolis flammea,* were 3—4 times more frequently caught in the stands without the shrub layer. Among many ichneumonid species parasitizing hosts associated with deciduous trees, only the proportion of *C. varipes* was higher in the stands with the shrub layer. *Also Ephialtes compuctor* and *E. quadridentatus* occurred almost exclusively in these stands.

Community V was distinguished for ichneumonids caught in the herb and shrub layers of the pine stands with the oak shrub layer and without the shrub layer, on the CF(1) site at Gościeradów. A total of 4.034 individuals representing more than 187 species were recorded.

The dominant species was *Lissonota variablis* (33.6%). The following species accounted for 2—7.5%: *Ichneumon subquadratus* (7.5%), *Proclitus autumnalis* (4.9%), *Exochus pictus* (4.5%), *Cratichneumon nigritarius* (3.3%), *Cymodusa atennuator,* and *Barycnemis gracilimus.*

Among the known parasites of insect pests, only *C. nigritarius* and *P. basizonus* reached relatively higher proportions, while *Polytribax arrogans, Barichneumon bilunulatus, B. praeceptor, Stenichneumon pictus* and *Exenterus* spp. were caught in smaller numbers.

Many species of more numerous *Ichneumonidae* are parasites of *Mycetophilidae,* or they are associated with the herb layer. Here such species can be mentioned as *L. variabilis* and *I. subquadratus,* the outbreak of which in the study area was probably related to the occurrence of a common host living, for instance, on lichens or mosses. The two species occurred on the coniferous forest sites and their proportions were always higher in the stands without the shrub layer.

Community VI involves *Ichneumonidae* caught in the herb and shrub layers in the pine stands with the oak shrub layer and without the shrub layer, on the CF(3) site at Kromnów. There were 382 individuals caught and they represented about 69 species.

Two dominant species were present in this community: *Barycnemis anurus* (8.4%) and *Proclitus grandis* (6.8%); the following species accounted for 3—5.2%: *Campoplex rothi* (5.2%), *Lissonota variabilis* (4.4%), *Oronothus* sp., *Cratichneumon culex* and *Spinolochus laevifrons.*

Proclitus sp., like in the other communities on the coniferous forest sites, were parasites of *Mycetophilidae.* The hosts of *Barycnemis* sp., *C. rothi* are little known; it is a parasite of lepidopterans living on shrubs and also occurs in agricultures. Like on the DF site, it was more abundant in the stand with the shrub layer, while in the stand without the shrub layer *Coccygomimus contemplator* and *Cratichneumon culex* were more frequently caught. These two species were probably more abundant there due to the presenc of birches in the upper layer of the stand, where their hosts occurred.

EFFECT OF THE SHRUB LAYER ON THE OCCURRENCE OF MORE IMPORTANT ICHNEUMONID SPECIES AND TROPHIC GUILDS IN PINE STANDS

The structure of trophic guilds of parasites and their role in controlling pest populations are determined by the bionomics of particular species, their relationships with hosts, and by a large number of biotic and abiotic factors influencing the development of both the host and the parasite. The family *Ichneumonidae* is very rich in species but, at the same time, their numbers in the areas where the outbreaks of phytophages do not occur are relatively low. This situation makes it difficult to analyse the effect of particular factors on different species of these parasites. Because of this reason it was decided first to analyse the effect of the shrub layer on more abundant species of economic importance, and then the guilds of parasites associated with definite hosts.

Cratichneumon nigritarius belong to more important parasites of *Bupalus piniarius* and *Panolis flammea*. The biology of this parasite is relatively well known but still not enough. Up to recent years this species has not always been distinguished from *C. culex* and *C. fabricator*, the main parasites of macrolepidopterans associated with deciduous trees. *C. nigritarius* were caught over the growing season. Two peaks of their numbers were observed (at the same time in the stands with and without the shrub layer), which would support the suggestion of many authors that this species has at least two generations a year. The female infests only pupae of lepidopterans occurring in litter. The larvae overwinter in host pupae. One generation of *B. piniarius* is attacked by two successive generations of this parasite; for the first time in autumn, and then the parasites emerging in early spring infest pupae of the host before the emergence of lepidopterans. For this reason the autumnal estimate of the infestation of *B. piniarius* population by *C. nigritarius* is not reliable. *C. nigritarius* is considered as an oligophagous or polyphagous species. It generally attacks pupae of lepidopteran pests, but is also known as a parasite of other lepidopterans of the families *Geometridae* and *Noctuidae*, which are associated with herbage, shrubs and deciduous trees. Hence, Eidmann [9] and other authors suggested that this parasite could reproduce more successfully in stands with diversified species composition.

C. nigritarius was the most abundant in the pine stands on the sites of coniferous forests (Fig. 7) where also the densities of pests were the highest. It was most frequently caught in lower layers; males fly closely to the herb layer in search of emerging females, and the females search for lepidopteran larvae in litter. The shrub layer had no effect on the population density of this parasite, which must depend on the density of *B. piniarius*. Only in the pine forest with the oak shrub layer the number of *C. nigritarius* was slightly lower than in the pine stand without the shrub layer on the same site, though the pest density was higher there. Also the richness of plant cover and habitat conditions on the DF site had no positive effect on *C. nigritarius* population at a low density of pine macrolepidopteran pests. However, the densities of *C. culex* and *C. fabricator*, which are closely related species with *C. nigritarius*, were high, so they had suitable hosts and developmental conditions there. These two species are rather accidental parasites of pine macrolepidopterans. They were most frequently caught in the pine stands on the DF and MCF sites, C. fabricator being also recorded on the CF(1) site in the stand with the shrub layer. More abundant occurrence of *C. culex* on the CF(3) site in the stand without the shrub layer was probably related to a small number of birches in the canopy, where this parasite could have its hosts.

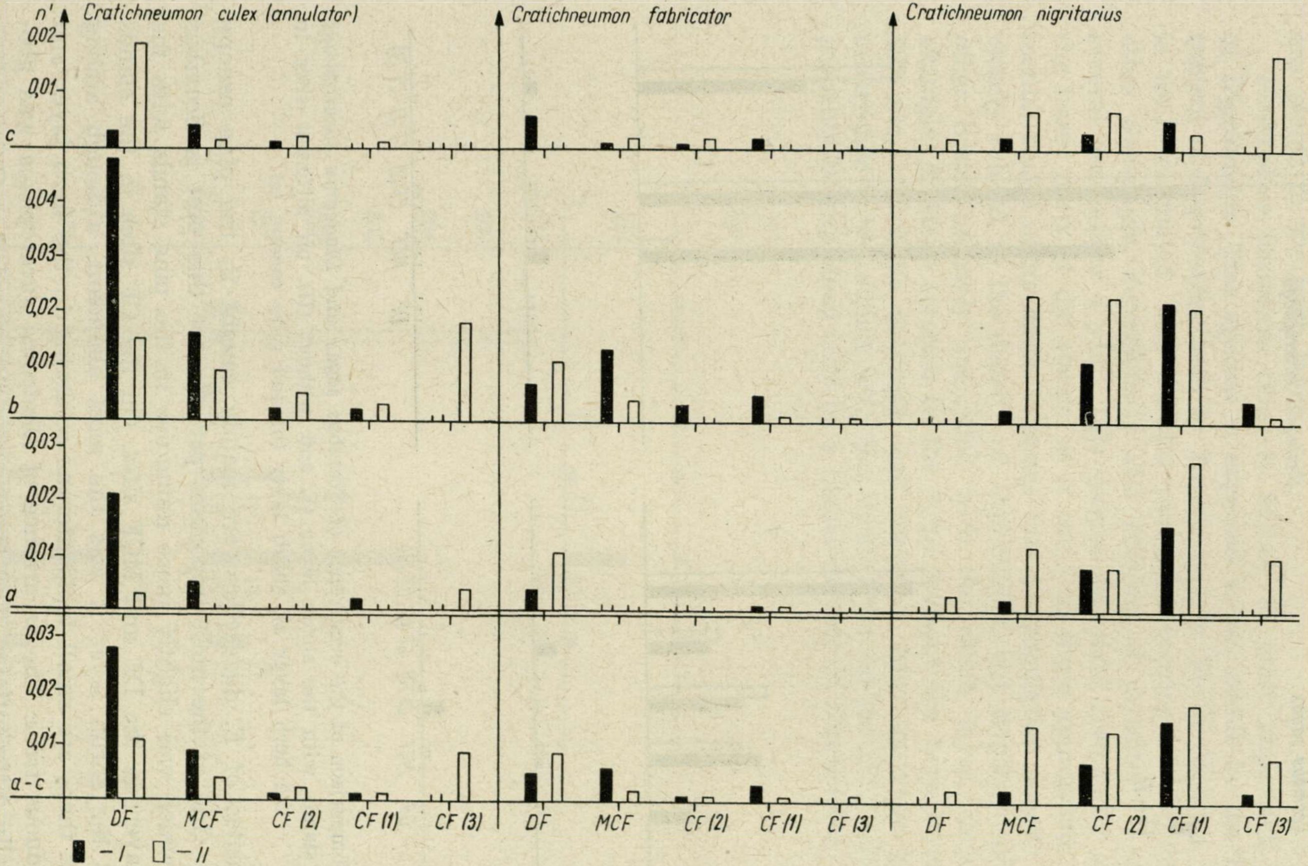


Fig. 7. Comparison of the occurrence of *Cratichneumon culex, C. fabricator* and *C. nigritarius* in pine stands with the shrub layer (I) and without (II), on different sites in the herb layer (a), shrub layer (b) and pine canopy (c), and the average values for the whole stands (a—c).

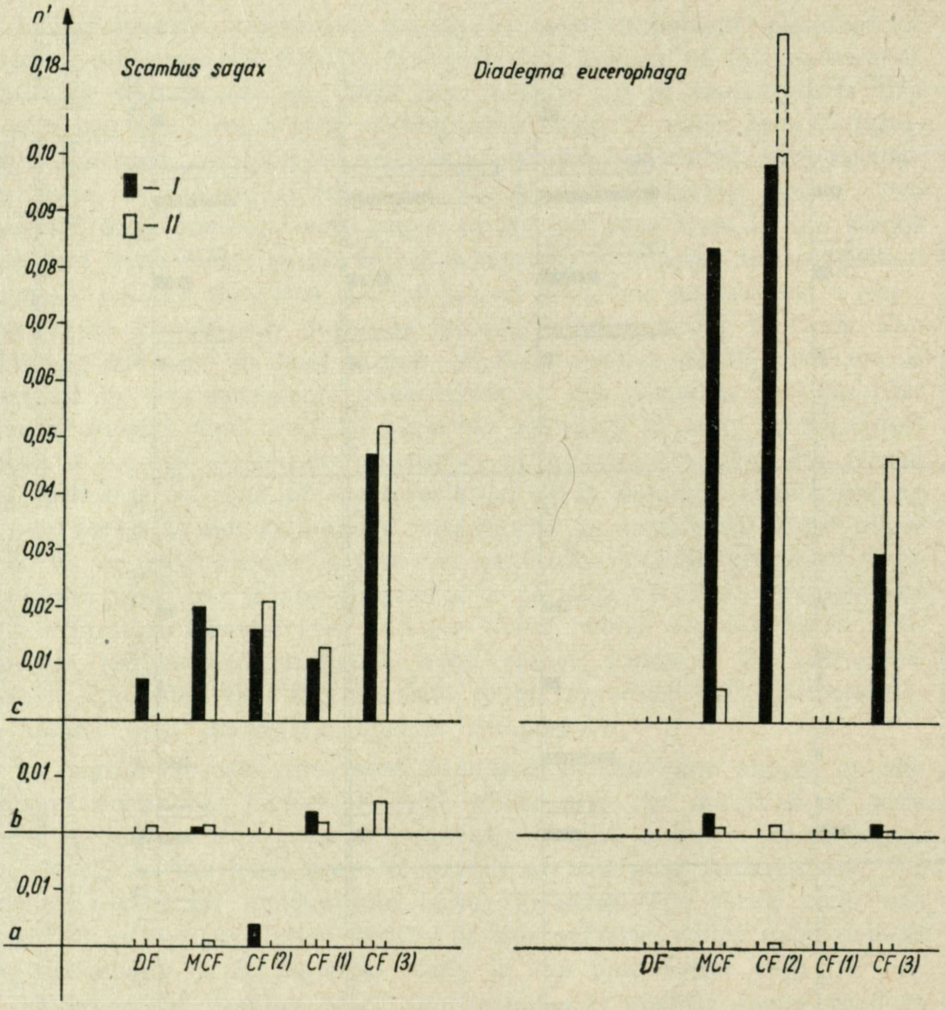


Fig. 8. Comparison of the occurrence of *Scambus sagax* and *Diadegma eucerophaga* in pine stands with the shrub layer (I) and without (II), on different sites in the herb layer a), shrub layer (b) and pine canopy (c).

Parasites of *E. dodecella* were mainly caught in the pine canopy (Fig. 8). One of the most important parasites of this pest is *Scambus sagax,* which was slightly more numerous in the pine stands with the shrub layer on the DF and MCF sites. On the CF sites in the stands without the shrub layer it was the most abundant, although among its hosts there are small lepidopterans occurring in the herb layer and on deciduous trees. The occurrence of *Diadegma eucerophaga* was geographically differentiated. This species was not recorded at Gościeradów. In the other regions it tended to occur like *S. sagax. D. eucerophaga* has recently been described and its biology is little known. In the pine canopy it could also have other hosts than *E. dodecella.* This parasite is known to emerge from larval lepidopterans associated with cruciferous plants in the herb layer.

Pleolophus basizonus (Fig. 9) belong to most important parasites of *Diprionidae*. This species is expected to be useful in the biological control of *Diprionidae* both in Europe and in North America where it is well acclimated. The females parasitize cocoons of *Diprionidae* or other *Symphyta*, occassionally also cocoons of parasites. It can have several generations a year. This species was most frequently caught in the lower parts of the stands, as it can find there appropriate developmental stages of its hosts. It seems that its population density was not closely related to the density of *Diprionidae*, but largely depended on other hosts, probably associated with the shrub layer, such as, for example. *Solidago serotina* in the stand without the herb layer on the DF site, where its outbreak was observed. Also its more numerous occurrence in the stands with the shrub layer on the CF(1) site cannot probably be explained only by a higher density of *Diprionidae*.

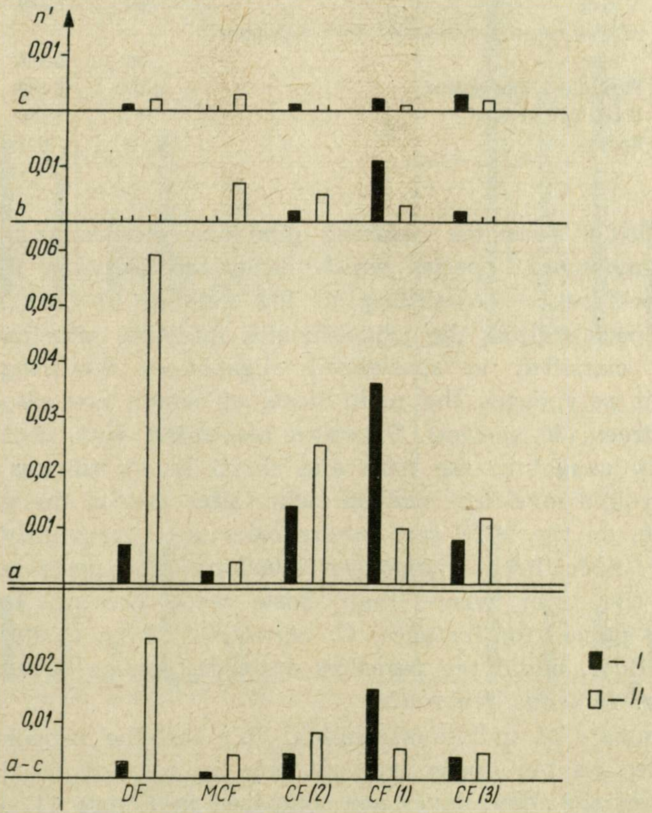


Fig. 9. Occurrence of *Pleolophus basizonus* in particular layers of the stands with the shrub layer (I) and without (II), on different sites (a — herb layer, b — shrub layer, c — pine canopy, a—c — average for the whole stand).

The classification of the *Ichneumonidae* caught to particular guilds of parasites associated with definite host groups was based on laboratory cultures and literature data. For the present analysis nine more important trophic guilds of *Ichneumonidae* have been selected (Tab. 3).

Table 3. Number of species (g) and individuals (n) of the *Ichneumonidae* that are potential parasites of particular hosts groups; the whole material for all the pine stands, collected by the trapping and sweeping methods

Hosts	*Ichneumonidae*	
	g	n
Macrolepidoptera associated with pine	44	1 928
Microlepidopteran pine pests	29	2 720
Diprionidae	24	676
Xylophages associated with pine	11	127
Macrolepidoptera associated with deciduous trees	64	1 849
Microlepidoptera associated with deciduous trees	39	2 388
Parasitic *Hymenoptera*	ca 90	1 149
Predatory insects	12	390
Spiders	ca 25	803

The guild of parasites reducing pine macrolepidopterans (Fig. 10) contains ichneumonid species which differ markedly in their biology and host preferences. According to the number of host species and degree of specialization, the ichneumonids infesting pine macrolepidopterans are classified to specialized oligophages attacking pests (14 species) and polyphages the main hosts of which are associated with deciduous trees (30 species). Parasites associated with deciduous trees were mainly caught in the herb and shrub layers (shrubs had leaves from the ground level up), and on richer sites also in the pine canopy; for instance, on the MCF site, where oaks were frequently present in the canopy. Specialized oligophages attacking pine pests generally occurred in the layer where their hosts were present. Ichneumonids parasitizing pupae, for instance, *C. nigritarius*, were mostly caught on the forest floor, while the parasites attacking larvae occurred in pine crowns (e.g. *Banchus femoralis)*.

The numbers of individuals caught (n′) and the proportions (u) of the parasites on pine macrolepidopterans in relation to the presence or absence of the shrub layer are compared in Figure 11. The number and percentage of polyphagous species, such as *Cratichneumon culex*, were higher in the stands with the oak shrub layer on the DF, MCF and CF sites, while in the stands with the beech shrub layer on the

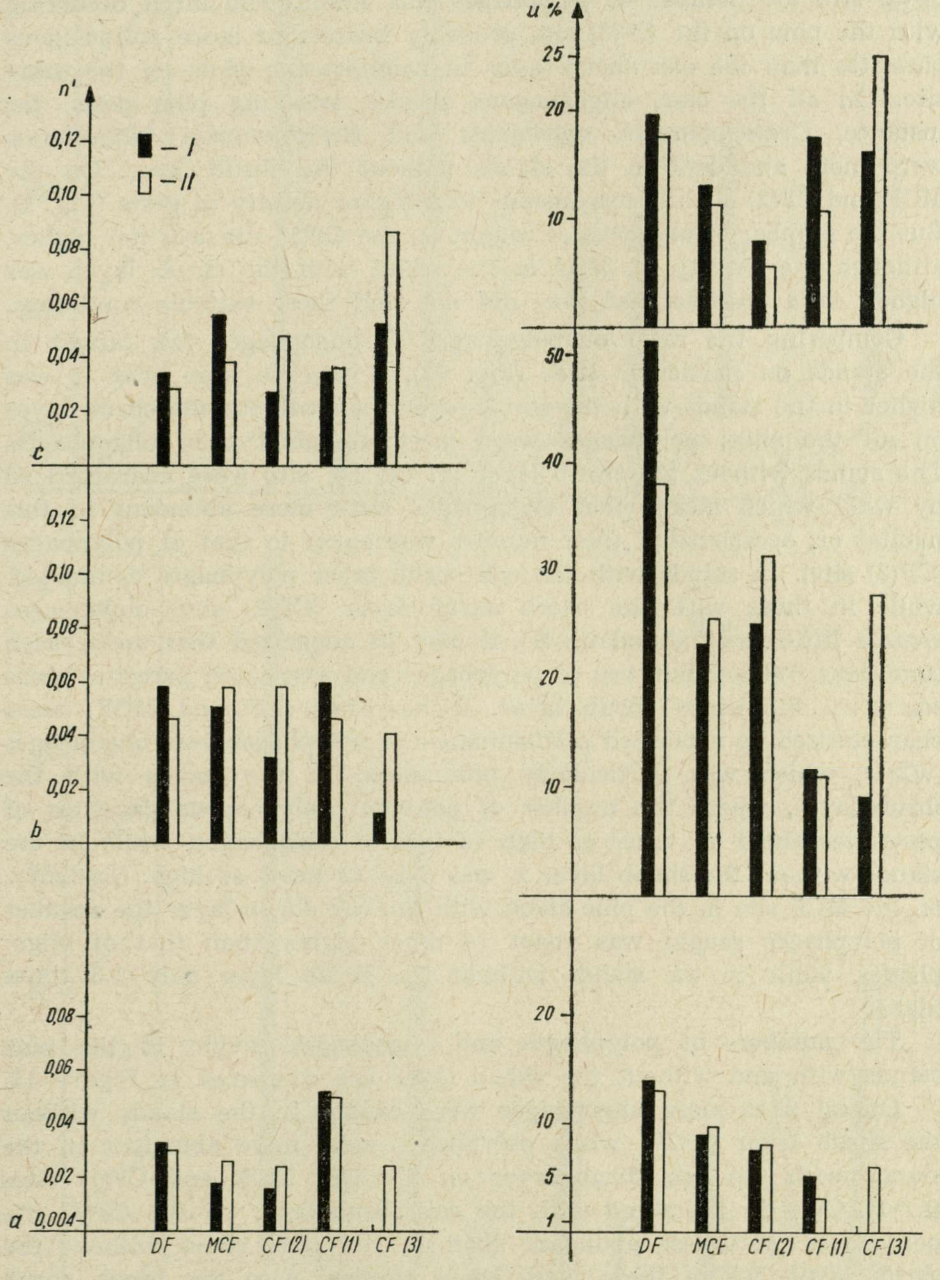


Fig. 10. Number of individuals (n') and proportion (u) of the ichneumonid guild parasitizing pine macrolepidopterans in particular layers (a — herb layer, b — shrub layer, c — pine canopy) of pine stands with the shrub layer (I) and without (II).

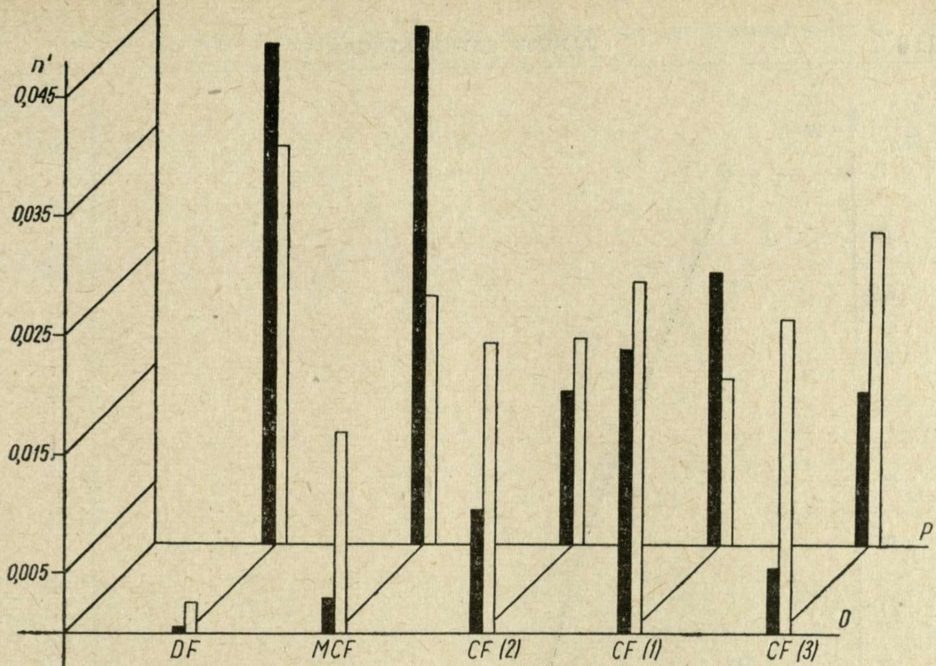
CF(2) site the number of polyphages was lower. The birch occurring with the pine on the CF(3) site probably introduced more polyphagous parasites than the oak shrub layer in neighbouring plots on the same site. On all the sites oligophagous species attacking pine pests, for instance, *Cratichneumon nigritarius* and *Barichneumon bilunulatus*, were more abundant in the stands without the shrub layer. On the MCF and CF(2) sites it corresponds to a higher density of pests (Fig. 2). But the number of oligophages caught on the CF(1) site was not higher, although the density of pests in the stand with the shrub layer was higher; it is possible that they did not find there suitable conditions.

Comparing the ratio of polyphages to oligophages (w) caught in the stands on particular sites (Fig. 12), it can be seen that it was higher in the stands with the shrub layer than without the shrub layer on all the sites; polyphages were more abundant than oligophages. The stands without the shrub layer on the CF site were characterized by $w \leqslant 1$ which means that oligophages were more abundant in this habitat or, occasionally, their number was equal to that of polyphages (CF(3) site). In stands with the oak shrub layer polyphages dominated, while in those with the beech shrub layer (CF(2) site) oligophages were a little more abundant. So, it may be suggested that under such conditions the communities of polyphages and associated parasites were scarce in the beech shrub layer. Richer sites (DF and MCF) were characterized by a marked predominance of polyphages over oligophages ($w > 1$), which was particularly pronounced in the stands with the shrub layer, where the number of potential polyphagous parasites of pests was about 70 times as high as that of oligophages, while in the stands without the shrub layer it was only 12 times as high. Similarly, on the MCF site in the pine stand with the oak shrub layer the number of polyphages caught was about 14 times higher than that of oligophages, while in the stands without the shrub layer only 1.3 times higher.

The numbers of polyphages and oligophages caught in the pine stands with and without the shrub layer are compared in Figure 13.

On all sites more oligophages were caught in the stands without the shrub layer ($k < 1$), while polyphages were more abundant in the stands with the oak shrub layer on the DF, MCF and CF(1) sites ($k > 1$). Only in the stand with the oak shrub layer on the CF(3) site polyphages were less abundant than in the pine stand without the shrub layer, where there were some birches. Also the beech shrub layer on the CF(2) site did not contribute to an increase in polyphages, as compared to the stand without the shrub layer on the same site.

The total number of *Ichneumonidae* species parasitizing pine macrolepidopterans was relatively similar in the plots with and without the shrub layer. Only the number of species caught in the stand with the



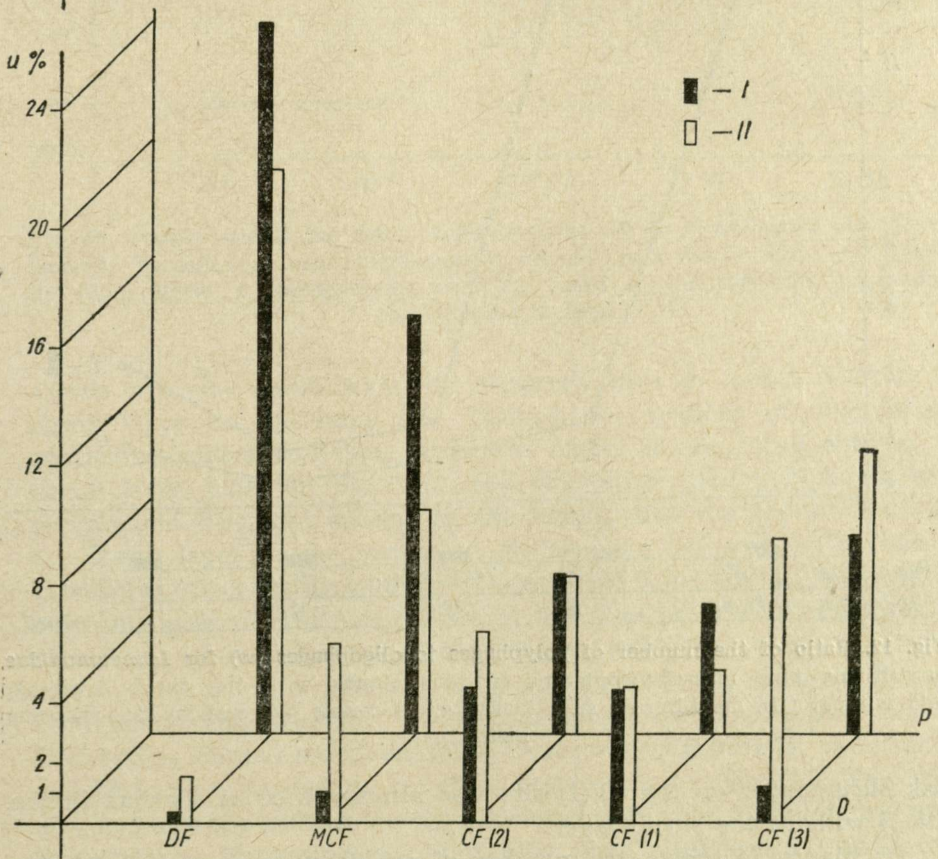
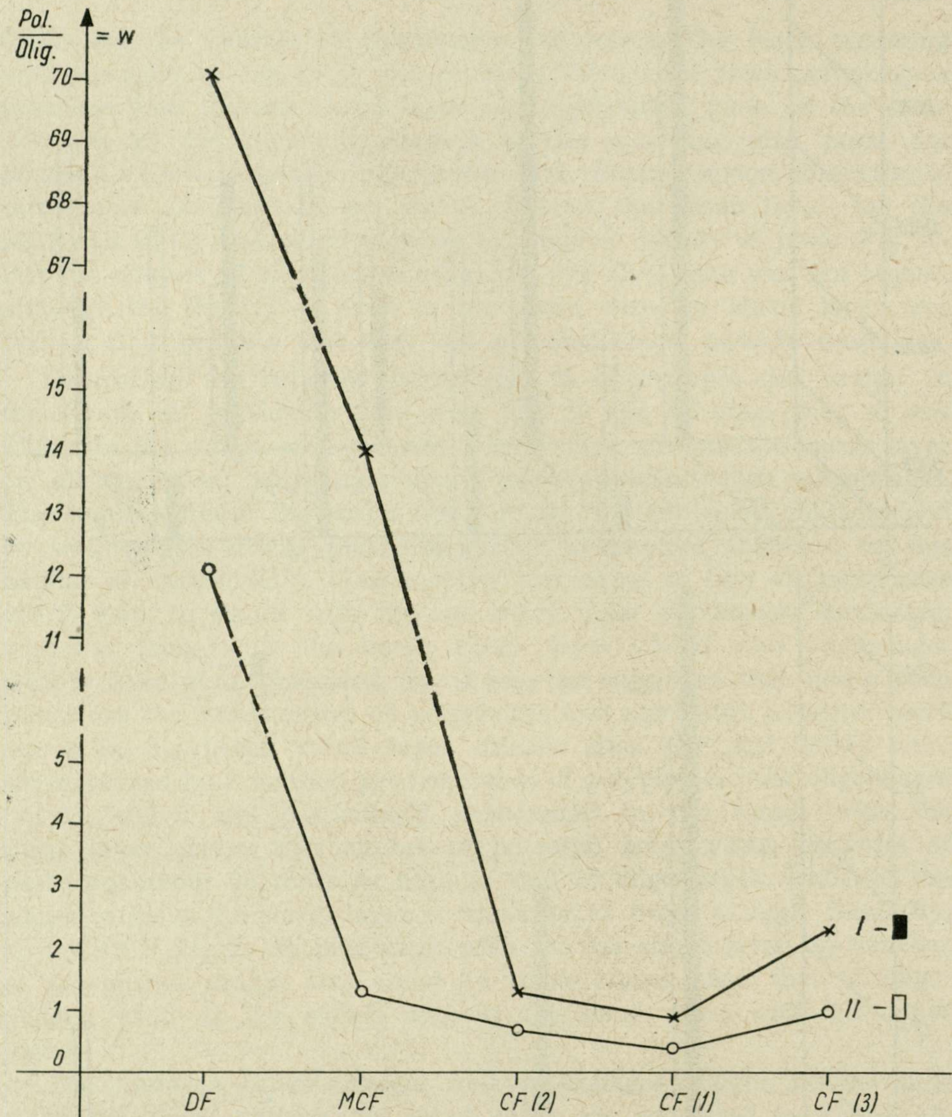


Fig. 11. Comparison of the number of individuals trapped (n') and proportion (u) of polyphagous (P) and oligophagous (O) *Ichneumonidae* that are potential parasites of pine macrolepidopterans in pine stands with the shrub layer (I) and without (II).



	DF I	DF II	MCF I	MCF II	CF (2) I	CF (2) II	CF (1) I	CF (1) II	CF (3) I	CF (3) II	
Polyphagous	141	97	140	85	45	62	75	49	14	42	No. of
Oligophagous	2	8	10	68	36	87	79	102	6	42	individ.

Fig. 12. Ratio of the number of polyphages to oligophages (w) for *Ichneumonidae* parasitizing pine macrolepidopterans in pine stands with the shrub layer (I) and without (II), on different sites (based on materials collected by the trapping method).

oak shrub layer on the CF(1) site was almost twice as high as in the stand without the shrub layer.

As Figure 14 shows, the number of polyphagous species of *Ichneumonidae* attacking pine macrolepidopterans was not higher in the

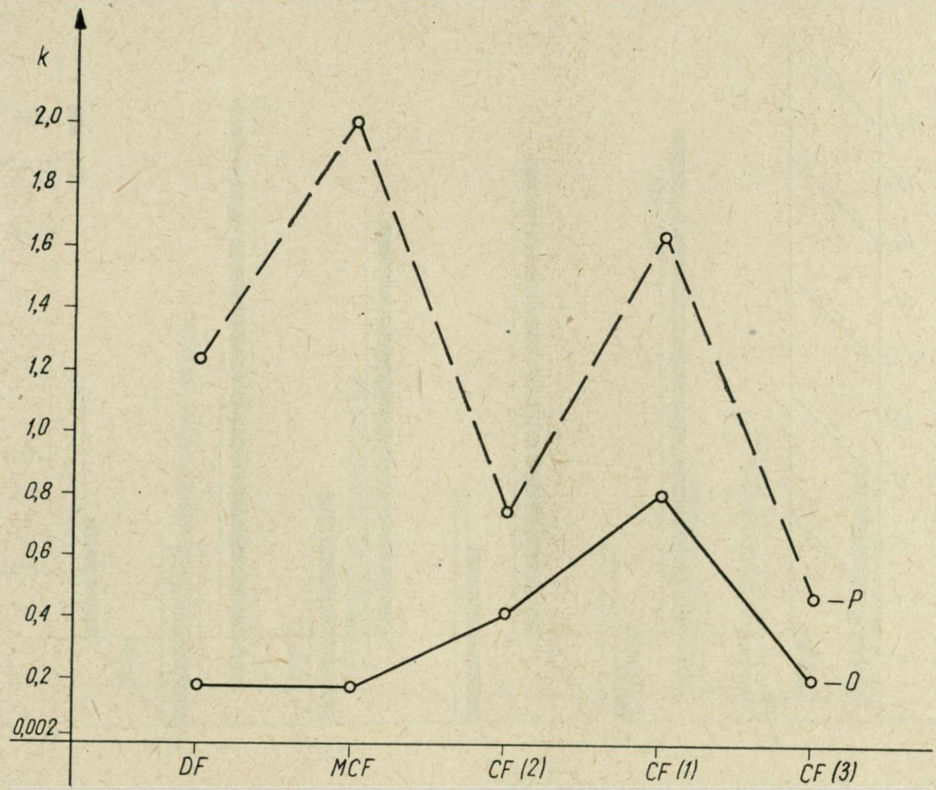


Fig. 13. Comparison of the ratio of polyphagous (P) to oligophagous (O) *Ichneumonidae* parasitizing pine macrolepidopterans in pine stands with and without the shrub layer on corresponding sites (k); based on the materials collected by the trapping method.

stands with the shrub layer, as compared with the stand without the shrub layer on the same site. Instead, the number of oligophagous species associated with pine pests was higher in the stand without the shrub layer. Only on the CF(1) site oligophages and polyphages were represented by more species in the stand with the shrub layer. So, the shrub layer in the stands on richer sites (DF and MCF) had no increasing effect on the number of species of polyphagous ichneumonids attacking pine macrolepidopterans. It had a positive effect only on the abundance of polyphagous species, for example, *C. culex*, on the DF site.

Ichneumonid parasites of microlepidopteran pine pests such as *Tortricidae*, *Exoteleia dodecella* and *Ocnerostoma piniarella*, were mostly caught in pine crowns, where their hosts occurred (Fig. 15). This guild also includes the species closely associated with pine microlepidopterans, for example, *Scambus sagax*, but they have also been recorded from other *Tortricidae*. In the stands with the oak shrub layer there were

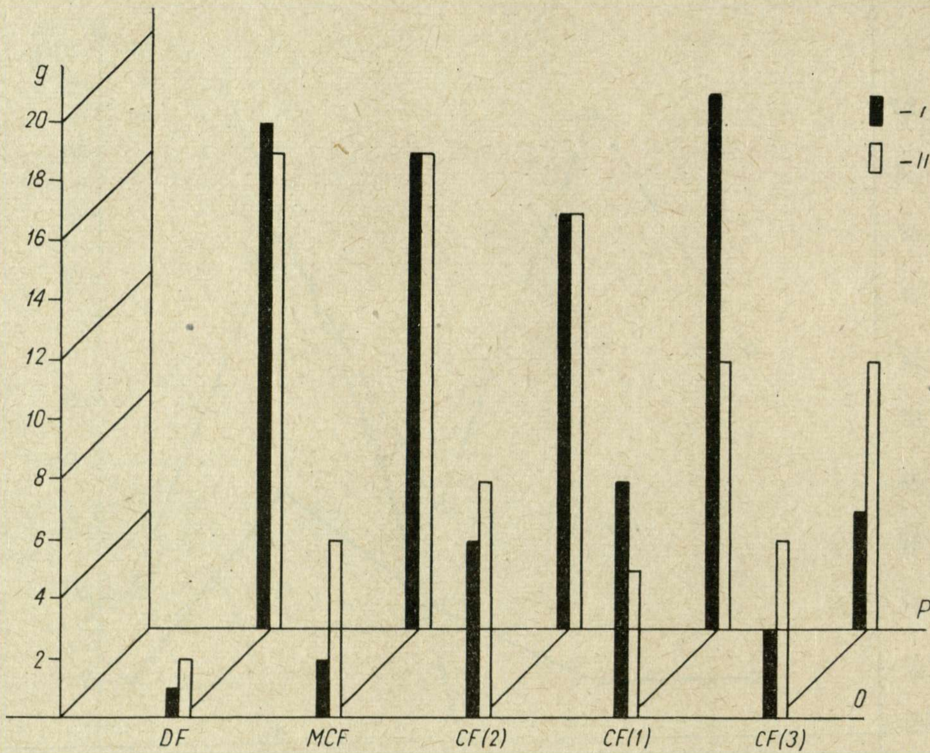


Fig. 14. Comparison of the number of species caught (g) of polyphagous (P) and oligophagous (O) *Ichneumonidae* that are potential parasites of pine macrolepidopterans in pine stands with the shrub layer (I) and without (II), on different sites.

more potential ichneumonid parasites of pine microlepidopterans, as compared with the stands without the shrub layer. Only on the CF(2) site with the beech shrub layer the number of parasites of these hosts was lower.

It is rather difficult to determine the factors controlling the ichneumonid guilds attacking *Diprionidae*. Parasites of *Diprionidae* have usually several generations over the year, and their populations can be large, independent of the density of *Diprionidae;* for instance, numerous occurrence of *Pleolophus basizonus* on the DF site in the stand without the shrub layer. The density of this guild in different layers and stands, with and without the shrub layer, varied considerably so that the role of the shrub layer cannot be precised.

Ichneumonid parasites of pine xylophages only occasionally have hosts in deciduous trees, and their density rather depends on hosts associated with pines, the density of the latter being related to the sanitary forest condition. Thus, it was difficult to determine the effect of the shrub layer on this parasite guild.

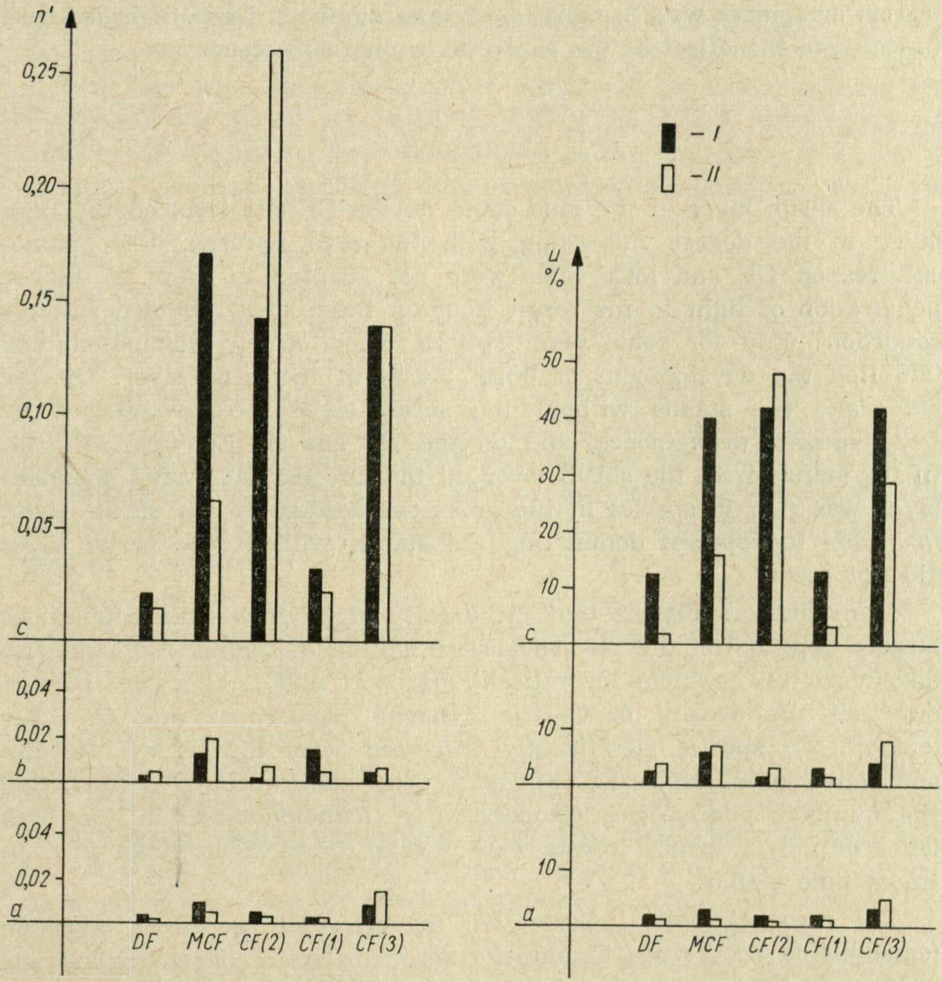


Fig. 15. Number of individuals (n') and proportion (u) of ichneumonid guild parasitizing pine microlepidopterans in particular layers (a — herb layer, b — shrub layer, c — pine canopy) of pine stands with the shrub layer (I) and without (II), on different sites.

The ichneumonid guilds infesting macro- and microlepidopterans associated with deciduous trees were more frequently caught on the DF and MCF sites in the stands with the shrub layer than without. On poorer sites (CF) they were more abundant in the stands with the oak shrub layer (CF(1) site) and in the stand without the shrub layer (CF(3) site), where there were some birches. In the stand with the beech shrub layer on the CF(2) site the number of parasites of *Lepidoptera* associated with deciduous trees was also lower.

Ichneumonids that are potential parasites of predatory and parasitic insects or spiders were caught in varying numbers. Thus, it is difficult to estimate the effect of the shrub layer on their occurrence.

DISCUSSION

The shrub layer in the pine stand on the CF site reduced the herb layer to the degree increasing with the area covered. Pine monocultures on DF and MCF sites were not adapted to them. A higher penetration of light to the forest floor on these sites provided suitable conditions only for some plant species. They largely dominated, and inhibited the development of other plants in the herb layer. On the MCF site the stands without the shrub layer were dominated by *Calamagrostis arundinacea,* and on the DF site by *Solidago serotina.* In the stands with the shrub layer on the DF and MCF sites the herb layer was rich in species in the areas overshaded by the shrub layer, in which the species dominating the stands without the shrub layer did not occur.

Many authors suggest that the density of phytophagous populations largely depends on the physiological condition of plants. Eidmann [10] developed this problem theoretically. Ruppert and Langer [40] pointed out that the density of *Tortrix viridana* populations and 60 other lepidopteran species significantly increased with higher soil fertility and water table. Ozols [32, 33] found, using the sweeping method, that the numbers and species composition of *Ichneumonidae* in the herb layer of mixed spruce forests were several times richer than in cup-moss pine stands.

The present results indicate that the effect of the shrub layer on ichneumonid occurrence in pine forests is different, depending on site conditions and on tree species in the shrub layer. A positive effect of the oak shrub layer on phytophagous *Ichneumonidae* that are potential parasites of insect pests was observed on richer sites (DF and MCF) and on the CF(1) site. The beech shrub layer on the CF(2) site was not favourable for more important ichneumonids.

Quantitative and qualitative comparison of all *Ichneumonidae* collected (Figs 3 and 4) shows that the numbers of individuals trapped on the DF and MCF sites were similar in the pine stands with and without the shrub layer, while on the CF site there were less individuals in all the stands with the shrub layer. The total number of species caught on the DF, MCF and CF(1) sites was higher in the stands with the shrub layer than without, while a lower number of species was caught in the stands with the beech shrub layer on the CF(2) site and with the oak shrub layer on the CF(3) site.

Therefore, a general view has been confirmed that more fertile and richer in plant cover forest sites, such as DF and MCF, are characterized by a greater species diversity of ichneumonid communities and, at the same time, by a lower density of particular species than the coniferous forest site such as CF(1) and CF(2). Conversely, the number of species on poorer sites was lower but some of them, for instance, *Lissonota variabilis* and *Ichneumon subquadratus*, were very abundant.

The analysis of Czekanowski's diagrams showed that the indices of similarity between the ichneumonid communities occurring in particular plots in lower parts of the pine stands with and without the shrub layer but situated on the same site were low, nevertheless, higher than the corresponding indices for the communities occurring in the stands situated on different sites. Taking this into account, in the lower parts of the stands various communities have been distinguished on different sites, while in the pine canopy only one on all the sites; it was very different from the communities occurring in the lower part of the stands.

The obtained results indicate that the layer is the most important factor controlling the structure of ichneumonid communities in pine stands. Site conditions, which influenced the richness of the herb layer, are on the second position. Thus, there was one community in the pine canopy, independent of the site, and different communities in lower parts (herb and shrub layers), depending on site conditions. The shrub layer only modified, particularly, on richer sites, the density of some species and guilds of species attacking particular hosts, but it could not completely change the structure of the community on a given site. The effect of geographical location and weather conditions cannot be analysed from the materials collected, but these factors should not considerably modify the effect of the shrub layer analysed in the present paper.

As the values of the indices of similarity were low, it was not possible to determine from Czekanowski's diagrams the effect of the shrub layer on ichneumonid communities within particular sites. So, the distinguished communities were used as units for which the occurrence of *Ichneumonidae* in the stands with and without the shrub layer on the same site was analysed as an average value for three plots.

It has been shown that particular ichneumonid species are closely related to definite site conditions. For instance, *Cratichneumon culex* and *C. fabricator* were mostly caught on the DF and MCF sites, while *C. nigritarius* on the MCF and CF sites, where its main host, *Bupalus piniarius*, occurred.

Pine stands with the oak shrub layer on the DF, MCF and CF(1) sites were characterized by higher numbers and larger proportions of parasites attacking micro- and macrolepidopterans associated with pines and deciduous trees, as compared with the pine stands without the shrub layer on the corresponding sites. Probably, the diversified species composition and rich herb layer on the DF and MCF sites were particularly favourable for the development of potential parasites of "primary" pine pests, even independent of their low density in the case of the DF site. It should be noted, however, that on the DF site only single specialized parasites of pine pests were caught, while the dominating species were polyphages associated with lepidopterans living on deciduous trees or in the rich herb layer. A favourable effect of the shrub layer on *Ichneumonidae* in the stands on the CF(1) site is likely to be also an effect of a relatively high water table. It could have a positive effect on the physiological condition of oaks and, due to this, on the number of hosts. In addition, the observations were made in a very hot summer, which could stimulate long-distance migrations of *Ichneumonidae* and also their assembling near the shrub layer.

The shrub layer in the pine stands on the DF and MCF sites had no effect on the total number of ichneumonid species parasitizing pine macrolepidopterans. Only the densities of some polyphagous species were higher, as compared with those in stands without the shrub layer. The oak shrub layer on the CF(1) site had a positive effect on the number of ichneumonid species associated with pine lepidopterans; both polyphagous and oligophagous species were caught in larger numbers. The beech shrub layer, however, had not a positive effect on the number of species associated with these hosts.

On the CF site (in the three localities) the ratio of polyphages to oligophages attacking pine macrolepidopterans was about twice as high as in the stands without the shrub layer, while on the MCF site it was ten times higher, and on the DF site 5.5 times higher. Thus, in the stands with the shrub layer the density of polyphages was generally a little higher than that of oligophages. In the stand with the beech shrub layer on the CF(3) site, the polyphages that are also parasites of pine macrolepidopterans were less frequently caught than in the stand without the shrub layer, while their proportions were similar in the two stands. This may indicate that the beech, which is not generally infested by many phytophages and reduces the herb layer with associated phytophages, cannot provide suitable conditions for such a large number of hosts which would be necessary for a more abundant occurrence of parasites than that observed in the natural herb layer on this site in the stand without the shrub layer. It also seems that a more abundant occurrence of polyphages in the stand without the shrub layer on the CF(3) site was due to the small number of birches in the main stand as some parasites could find there appropriate hosts. In the stand with the oak shrub layer the hosts must have been relatively less abundant.

In sum, it may be suggested that the deciduous shrub layer, particularly beech, in pine stands on the sites of coniferous forests has not a positive effect on ichneumonid parasites attacking insect pests. Only the oak shrub layer on the CF(1) site had a positive effect on the density and species composition of polyphagous *Ichneumonidae*. This effect, however, was not so pronounced as in the stands on richer sites; the number of polyphages in the stand with the shrub layer on the CF(1) site was reduced by half and their proportion was reduced to one-sixth of the values in the stands with the shrub layer on the DF site (Fig. 11). This is probably related to the fact that deciduous species living under conditions considerably different from the optimum (unsuitable site, overshading by the main stand) are not abundantly inhabited by host insects. In addition, the microclimate on the forest floor is modified in the presence of the shrub layer in such a way that it has a limiting effect on the herbage cover characteristic of the site, and on the associated entomofauna. It is possible that on the coniferous forest site more parasites can find hosts on birches than on oaks (CF(3) site).

A favourable effect of the deciduous shrub layer in the pine stands was observed on the DF and MCF sites, where relatively larger numbers of *Ichneumonidae* were caught, mostly polyphagous, that are potential parasites of insect pests. This must be related to the fact that the deciduous shrub layer on optimal sites, together with the rich plant cover on the forest floor, is inhabited by many hosts of different species, and this creates favourable conditions for many parasites with complex trophic chains. In the stands with the species composition corresponding to site conditions there are close relationships among the vegetation, phytophages and parasites. These relationships are characteristic of particular site conditions, and become more and more complicated with increasing richness of the habitat.

It seems that efforts made to improve the natural resistance of stands to insect pests should be directed towards improving site conditions, for instance, by the application of fertilizers or the modification of soil moisture conditions. Deciduous species introduced into poorer stands are foreign components in these communities, thus they can disturb biocoenotic relationships developed by evolutionary processes occurring in them, which was probably the case of the beech shrub layer.

From the point of view of parasitic insects *(Ichneumonidae)* the shrub layer should be introduced into rich sites with respectively high water table, for instance, along running waters or in depressions of the ground.

CONCLUSIONS

1. Almost 680 ichneumonid species were recorded in particular layers of pine stands on the DF, MCF and CF sites in Poland.

2. In the pine canopy occurred only one ichneumonid community, independent of the type of the site. Characteristic and most abundant species were: *Diadegma eucerophaga, Scambus sagax, Trychosis legator, Macrus parvulus, Gelis areator, Idiogramma euryops, Tersilochus* sp., *Adelognathus* sp., *Phaeogenes vagus, Nemeritis caudatula, Eriplastys ardeicollis,* and *Clistopyga canadensis.*

3. In the lower part of the stands (herb and shrub layers) the structure of ichneumonid communities depended on the site. *Cratichneumon culex* was the dominant species on the DF site, one species of the genus *Eusterinx* on the MCF and CF(2) sites, *Lissonota variabilis* on the CF(1) site, and *Barycnemis anurus* and *Proclitus grandis* on the CF(3) site.

4. The shrub layer artificially introduced into the forest had no effect on the species composition of ichneumonid communities, but only modified the density of some species in the lower part of the stands.

5. The shrub layer had not a positive effect on the population density of *Cratichneumon nigritarius.* The populations of *C. culex* and *C. fabricator* were considerably higher in the stands on rich sites (DF and MCF), and generally more abundant in the stands with the shrub layer. The occurrence of *Pleolophus basizonus, Scambus sagax* and *Diadegma eucerophaga* was not related to the presence of the shrub layer.

6. The oak shrub layer had a positive effect on the density of trophic guilds of the *Ichneumonidae* that are potential parasites of *Macrolepidoptera* and *Microlepidoptera* associated with pines and deciduous trees. This was not the case of the beech shrub layer on the coniferous forest site.

7. The total number of ichneumonid species attacking pine microlepidopterans was very similar in the stands with and without the shrub layer on each site.

8. The number of polyphagous species parasitizing pine macrolepidopterans was generally similar in the stands with and without the shrub layer. But the number of oligophagous species was usually higher in the stands without the shrub layer.

9. The density of polyphagous *Ichneumonidae* parasitizing pine macrolepidopterans was higher in the stands with the oak shrub layer and increased with the richness of the site. The number of oligophages, however, was higher in the pine stands without the shrub layer on all sites.

10. Therefore, the effect of the shrub layer on *Ichneumonidae* was differentiated, depending on the site, the layer and the species composition of the shrub layer.

11. On all sites the introduction of the oak shrub layer into pine stands without the shrub layer is very useful from the point of view of the *Ichneumonidae* that are potential parasites of pine pests, but on more fertile sites this effects is many times increased.

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WPŁYW PODSZYTÓW NA WYSTĘPOWANIE *ICHNEUMONIDAE (HYMENOPTERA)* W DRZEWOSTANACH SOSNOWYCH NA RÓŻNYCH SIEDLISKACH

STRESZCZENIE

Metodą żółtych naczyń i „koszenia" czerpakiem zebrano w drzewostanach sosnowych 12 203 okazy *Ichneumonidae* należące do blisko 680 gatunków. Zagęszczenie szkodników sosny ustalono na podstawie jesiennych poszukiwań w ściółce.

Pierwszoplanowym czynnikiem decydującym o strukturze zgrupowań *Ichneumonidae* w drzewostanach sosnowych jest warstwa drzewostanu, na drugim miejscu znalazły się warunki siedliskowe. W związku z tym wyodrębniono jedno zgrupowanie dla koron sosen, bez względu na typ siedliska oraz różne zgrupowania dla dolnej partii drzewostanów związane z określonymi siedliskami — tyle zgrupowań, ile badanych siedlisk.

W koronach sosen wszystkich siedlisk około 30% osobników stanowiły pasożyty *Microlepidoptera* sosny (dominant *Diadegma eucerophaga*), 4% pasożyty *Macleropidoptera* sosny i boreczników, około 8% pasożyty owadów drapieżnych i pajęczaków.

Podszyty liściaste w drzewostanach sosnowych wszystkich badanych siedlisk, w porównaniu z drzewostanami bez podszytów, nie wpłynęły na zwiększenie liczebności populacji *Cratichneumon nigritarius, Pleolophus basizonus, Scambus sagax* i *Diadegma eucerophaga*.

Podszyty dębowe wywierają pozytywny wpływ na liczebność gatunków niewyspecjalizowanych w stosunku do szkodników sosny, np. na *Cratichneumon fabricator, C. culex*. Zjawisko to zaznaczyło się znacznie mocniej na siedliskach bogatszych, niż w ubogich borach. Natomiast wyspecjalizowane pasożyty szkodników sosny posiadały większą liczebność w litych drzewostanach sosnowych.

ВЛИЯНИЕ ПОДЛЕСКА НА ВСТРЕЧАЕМОСТЬ *ICHNEUMONIDAE* (*HYMENOPTERA*) В РАЗНЫХ БИОТОПАХ СОСНОВОГО ДРЕВОСТОЯ

РЕЗЮМЕ

В трех ярусах соснового древостоя собрано 12 000 особей *Ichneumonidae*, принадлежащих к около 680 видам. Структура сообществ зависит от яруса древостоя и условий биотопа; влияние подлеска незначительно. 30% особей, встречающихся в кронах сосен, — это паразиты *Microlepidoptera* сосны (доминирующий вид — *Diadegma eucerophaga*), 4% — паразиты *Macrolepidoptera* и *Diprionidae* сосны, 8% — паразиты хищных насекомых и пауков, *Aranei*. Автор проанализировал влияние подлеска на *Cratichneumon nigritarius, C. fabricator, C. culex, Pleolophus basizonus, Scambus sagax* и *Diadegma eucerophaga*, а также 9 трофических комплексов. Констатировано положительное влияние дубового подлеска на встречаемость полифагических видов, и, чем богаче был биотоп, тем это влияние было сильнее.