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THE EFFECT OF FOREST-FIELD ECOTONES ON BIODIVERSITY OF ENTOMOFAUNA AND ITS FUNCTIONING IN AGRICULTURAL LANDSCAPE

ABSTRACT: Reactions of various entomofauna groups to the environmental conditions of forest-field ecotones were investigated. An increase in insect biodiversity in the ecotone zone was found. The intensity of the seasonal exchange of insects between the forest and open areas was assessed. Conditions under which the ecotone became for insects either a transition zone or an untraversable barrier were determined. Attention was directed to the special importance of ecotones for insects migrating from crop fields during intensive agrotechnical treatments (e.g. ploughing).

KEY WORDS: landscape structure, ecotones, dispersion, migrations, insects, Diptera, Chloropidae.

1. INTRODUCTION

The increasing interest in ecotone problems is due mainly to two causes. On the one hand, this interest results from the recent years' intensive development of the theoretical foundations of landscape ecology, which consider the ecotones to be one of the essential elements of the spatial structure and to be decisive of the functioning of natural systems on a scale of the landscape. On the other hand, this interest is caused by the fact that human impact manifests itself, among others, by an increase in the number and length of ecotones as well as by a rise in the mosaic of environments and landscape. In this connection it is necessary to give some thought to the consequences of these phenomena for the agricultural and forestry practice, landscape management etc. (Forman and Godron 1986, Di Castri et al. 1988, Holland et al. 1991, Hansen et al. 1992).

Thus, on practical and theoretical grounds the problems of the transition zones between two natural systems are at present of great interest to biologists of various specialities. Ecotone problems under study concern the specificity of the ecotones as habitats for various groups of organisms as well as involve the significance of this zone for determining the directions and intensity of the exchange of individuals, species, biomass and energy between the landscape structure elements (Di Castri et al. 1988, Hansen et al. 1992, Ryszkowski and Bałazy 1992).

In the literature the significance of the ecotones for animals has most often been evaluated with respect to the vertebrates whereas on methodological grounds the invertebrates were much less often the object of relevant studies (Łuczak et al. in print). Therefore it is important to collect information on the reactions of the invertebrates to ecotones (which undoubtedly in many cases differ from the reactions of the vertebrates), as well as to utilize these data for formulation of theoretical assumptions concerning the significance of the ecotones for landscape structure and functioning.

The aim of the present studies was to assess the effect of the ecotones, formed in the agricultural landscape between small forest islands and crop fields, on the dispersion of the entomofauna, its diversity and exchange between the forest and agricultural ecosystems.

It is stressed that the forest-field systems are very widely spread landscape structures; the transition zones formed in these systems are characterized by connecting two different ecosystems: the stable and usually equilibrated natural forest environment and the agroecosystem changing intensively as a result of human activities both during the vegetation season and from year to year. In such ecological conditions the exchange of biological material across the ecotone zone between the forest and crop field is particularly intensive.

It is necessary to specify very accurately the object of studies, because in the literature the term "ecotone" is applied to very dissimilar natural systems, beginning from the margin zones of biomes and ending on the contact zones between environmental patches formed e.g. within the forest herb layer (Hansen et al. 1992, Holland et al. 1991, Bunce et al. 1993).

The kind of the environments forming the transition zone is of importance, because according to the definition of ecotone, generally accepted in ecology (Di Castri et al. 1988), it is a transition zone between two natural systems which are decisive of its essential properties. Thus, the character of the whole ecotone system determines the specificity and significance of the ecotone, e.g. it settles whether the ecotone is mainly a transition zone (when both environments are very similar) or acts as a barrier (in the case of very dissimilar environments) for transitions of many groups of organisms.

As for as the present studies are concerned, the environment system: forest-ecotone-field, is a terrain of particularly intensive migrations of animals including also

insects (Dąbrowska-Prot 1991). Agrotechnical treatments of various types (chemicalization, ploughing etc.), performed in agricultural ecosystems, and varying microclimatic conditions force the insects to migrate periodically from crop fields to the interior of forests or only to their ecotones (Melnichenko 1949). Observations of the phenomena of this type, taking place between the forest and crop field, allow for more complete evaluation of the significance of the ecotones for insects, as compared with the information obtained in the case of the contact zone between two less dissimilar terrestrial ecosystems, e.g. of the forest-forest type.

2. TERRAIN OF STUDIES, METHODS AND INSECT MATERIAL

The present studies amplify our earlier published analysis of the role of forest islands in the agricultural landscape (Dąbrowska-Prot et al. 1991). Among eight forest islands, investigated in the years 1986–1987, four were selected for the present ecotone studies performed in the years 1988, 1989 and 1991 (Fig. 1, forest islands nos. 1, 3, 5 and 7).

The permanent terrain of the present 3-year studies consisted of the ecotone transect which included a 1-ha, nearly 100 years old forest island of the Pino-Quercetum type (forest island no. 5) and the adjacent crop fields (winter rape and winter barley plantations). This provided an insect material allowing for evaluation of the unchangingness of the phenomena taking place in the ecotone. Moreover, each year – apart from the above mentioned ecotone transect – another additional transect was studied: in 1988 – one with a 1.5-ha birch-aspen woodlot developing spontaneously on barrens (forest island no. 5) and adjacent crop-fields (winter barley); in 1989 – one with a ca. 1.0-ha birch-aspen woodlot (forest island no. 7) and adjacent fields; in 1991 – one with a 35-ha forest island of the Pino-Quercetum type (forest island no. 1), that before several decades has constituted one forest complex with the 1-ha forest island no. 3 and adjacent field. This selection of the transects enabled evaluation of the effect of the principal factors, i.e. origin and size of the forest island, on the differentiation of the ecotone zones and their role in the ecological phenomena and processes in the landscape.

According to the applied method, within a ca. 300–400 m space between the forest island interior and adjacent crop field interior 4 zones were singled out: 1) forest interior, 2) forest margin (a ca. 3–4 m wide belt, always with southern exposure), 3) crop field margin (a ca. 1–2 m wide belt) and 4) crop field interior.

Environmental observations pointed to evident differences between the margin parts and interiors of the ecosystems in the microclimatic conditions, as well as in the vegetation composition and denseness. Thus it was found appropriate to consider the margin parts of forest and field to be transition zones between the typical forest and field ecosystems. Evaluation of the width of the transition zones and botanical characterization of all of the four zones were based on phytosociological records (Wójcik 1991, Wójcik and Wasilowska 1995).



Fig. 1. Distribution of forest islands in the landscape
1-4 Pino-Quercetum forests, 5-8 birch-aspen woodlots

In the different zones of the transects microclimatic studies were performed; they included measurements of the temperature and air humidity in the vegetation layer: next to the ground and at a 2-m height.

In the four singled out zones of the transects, the insects were caught with an entomological sweep-net. Catches were performed once monthly from April (snow thaw) until November (first ground frosts). In each zone of the transects a series of 10 samples was taken; one sample included the insects caught upon 25 sampler strokes (this afforded insect numbers). In some cases, for comparative purposes, it was necessary to calculate the results per area unit. On the ground of the literature

data (Melničenko 1949, Gilarov 1965) and own results (Dąbrowska-Prot 1991) it was assumed that one series of 10 samples provides the insect material from 60 m² (this afforded insect density). Furthermore, the biomass (dry weight of insects) was determined; the mean biomass of an individual was obtained by dividing the total biomass of insects by their number.

The collected material was identified to orders. The Diptera which were the most numerous groups of insects (they accounted for 45–ca. 60% of the local entomofauna) were analyzed to families. The Chloropidae family which was dominant among the Diptera (up to 20%) and included important pests of cultivated and wild plants was identified to species. In the case of some orders, e.g. the Heteroptera and Coleoptera, certain families of ecological or practical importance were distinguished.

All of the insect groups singled out on account of various biological features were regarded as indicators of the reaction of definite ecological groups of organisms to ecotone conditions. For example, the dispersion of the Culicidae family (Diptera) emerging in water bodies was regarded as an example of the reaction of migrants to ecotones, and the distribution of the Chloropidae – as the reaction of the group representing mainly the phytophagous insects of plant cultures.

3. RESULTS

3.1. HABITAT CHARACTERIZATION OF THE ECOTONES

Microclimatic and phytosociological data pointed to a clear-cut habitat diversity of ecotones and interiors of the ecosystems which form them (Wójcik 1991, Wójcik and Wasilowska 1995). As an example, Table 1 shows the values of temperature and relative air humidity in the forest herb layer and brushwood layer in two different periods of the vegetation season (early spring and early summer); these values testified to substantial microclimatic differentiation of the transect zones.

The properties of the microclimate prevailing in the margin parts of the forest and field were characterized by the following regularities: 1) in the ecotones, as compared with the interiors of forest and field, the temperature was usually higher and air humidity-lower (in the ecotones of the Pino-Quercetum forest islands and birch-aspen woodlots); 2) in the ecotones the climatic differences between the forest herb layer and brushwood layer were more pronounced (the latter layer was usually drier); 3) in the ecotones the daily fluctuations in the values of the climatic parameters were greater (Wójcik and Wasilowska 1995).

It may thus be assumed that the ecotone zone as compared with the interior of the ecosystems, represents from the standpoint of the climate a more variable habitat, with a sharper slope of the temperature-humidity gradients; this may affect adversely many groups of organisms, particularly the poikilothermic ones. On the other hand, in the low-temperature periods (particularly in spring and autumn) the

ecotones form in the forest-field landscape patches of better sun-heated, warmer and drier habitats with cumulation of the entomofauna which is sparse at these times (Table 1).

Table 1. Microclimatic conditions in the ecotone transect with 1-ha Pino-Quercetum forest island and adjacent crop field (winter barley) in two different periods of the vegetation season: early spring and full summer

Zone	Season							
	24 Apr. 1991 11–12 a.m.				12 June 1991 11–12 a.m.			
	Forest herb layer		2 m		Forest herb layer		2 m	
	Temp. (° C)	Humidity (%)	Temp. (° C)	Humidity (%)	Temp. (° C)	Humidity (%)	Temp. (° C)	Humidity (%)
Forest interior	10.25	63	8.00	59	14.5	78	15.0	60
Forest ecotone	16.50	51	10.50	57	15.0	63	15.5	63
Field ecotone	14.50	57	11.50	57	24.0	68	20.0	63
Field interior	12.50	60	10.50	58	19.0	59	18.0	62

Studies of the vegetation in ecotone transects: from the forest island interior across the forest ecotone and field ecotone to the crop field interior, indicated that the margin parts of the forest and field (3–4 m and 1–2 m in width, respectively), were inhabited by distinct plant associations which differed from the vegetation of the interiors of the forest (particularly in the case of the Pino-Quercetum forest islands) and crop field ecosystems in the richness of species belonging to various ecological groups; frequently, in the ecotones the density of these species was high (Wójcik 1991, Wójcik and Wasilowska 1995). This is due, among others, to intensive penetration of many wild plants characteristic of fields into the forest ecotone, and *vice versa* – to penetration of some forest species into the field ecotone.

Obviously, the specific microclimatic conditions and character of the ecotone vegetation lead to differentiation of the fauna, particularly insects which very strongly react to environmental conditions by changes in dispersion. Thus it may be inquired what is the significance, for the entomofauna (its numbers, biodiversity, dispersion in the landscape, periodic migrations etc.), of the ecotone zones formed between the stable forest ecosystems and crop field ecosystems which change intensively during the vegetation season.

3.2. ECOTONES AS A SPECIFIC HABITAT FOR THE ENTOMOFAUNA

3.2.1. Numbers and biomass distribution pattern of insects

The 3-year studies performed in the ecotone transect with a 1-ha forest island (no. 3) of mixed forest, located among crop fields (winter rape cultures), pointed to great differences between the various transect zones in the entomofauna. The positive reaction of insects to ecotones manifested itself in the first place by their

greater biomass and numbers in this habitat (Table 2). The entomofauna and Diptera biomass in both ecotone zones accounted for 79 and 56%, respectively, of the total biomass in the transect; in the case of the numbers of those groups, the respective values were 55 and 45% (Table 2). The same habitat preferences of insects came to light upon detailed analysis of the results obtained in 1989 and 1991 (Table 3).

Table 2. Numbers and biomass distribution patterns (in % of the total numbers and biomass in the transect) of the entomofauna and Diptera along the ecotone transect: 1-ha Pino-Quercetum forest island-forest ecotone-field ecotone-field, as well as the mean individual weight. The differentiation degree of insect colonization of the transect zones was evaluated by the coefficient of variation (3-year studies)

		Distribution		Mean individ. weight mg dry wt indiv. ⁻¹	
		Insects	Diptera	Insects	Diptera
Numbers	Forest	27	31		
	Ecotones-forest	30	25		
	Ecotones-field	25	20		
	Field	18	24		
Coefficient of variation		0.195	0.174		
Biomass	Forest	16	26	1.432	0.883
	Ecotones-forest	39	28	2.333	1.073
	Ecotones-field	40	28	2.710	1.461
	Field	5	18	0.950	0.760
Coefficient of variation		0.536	0.161	0.435	0.294

The intensity of fauna cumulation in the ecotones failed to be related directly to the total fauna abundance in a given year. This was indicated by e.g. the fact that during the 3-year studies the difference between years in entomofauna numbers in the whole terrain amounted to 3.5% whereas at the same time the respective difference in the intensity of insect colonization of the forest ecotone attained 11.5% and that of the field ecotone – as many as 30%.

In the consecutive years of studies, significant differences in colonization between the different zones of the ecotone transect (Friedman's test, Siegel 1956) were found for the numbers ($p < 0.001$) and biomass ($p < 0.05$) of the total entomofauna and for Diptera biomass ($p < 0.05$). Differences in Diptera numbers between the various zones of the transect were not significant.

The fact that in the forest and field zone of the ecotone insect biomass exceeded that found for the interior of both ecosystems was related, among others, to the local occurrence of individuals of a greater body weight (Table 2). This was particularly evident in the case of the field ecotone where during 3 years of studies the mean individual body weight was 2–3 times greater than in crop field interior.

In 1991 simultaneous studies were carried out in two transects differing in size of the Pino-Quercetum forest islands (1 and 35 ha, respectively) being transect components; both forest islands were separated by a ca. 300-m wide crop field belt. It was found that in both transects insect distribution was similar (similar values of the coefficient of variation that is the ratio of standard deviation to the mean (Table 3), despite the differences in total numbers (by 12%) and biomass (by 3%) between the entomofauna inhabiting these transects. In the forest and field ecotones adjoining the 1-ha forest island, 63% of the total numbers of insects and 78% of the total biomass were cumulated; for the ecotones adjacent to the 35-ha forest, the respective values were 65 and 77.5% (Table 3).

Table 3. Numbers and biomass distribution patterns (in % of the total numbers and biomass in the transect) of the entomofauna and Diptera in ecotone transects differing in forest island size (studies in 1991) and forest island origin (studies in 1989). The differentiation degree of insect colonization of the transect zones was evaluated by the coefficient of variation

	Numbers				Coefficient of variation	Biomass				Coefficient of variation
	Forest	Ecotones		Field		Forest	Ecotones		Field	
		forest	field			forest	field			
1991										
Transect field – 1-ha Pino-Quercetum (forest island no. 3)										
Entomofauna	26	34	30	10	0.404	19	34	42	5	0.660
Diptera	29	30	25	16	0.238	26	28	32	14	0.296
Transect field – 35-ha Pino-Quercetum (forest island no. 1)										
Entomofauna	28	32	34	6	0.502	19	37	41	3	0.692
Diptera	22	24	43	11	0.527	22	27	38	13	0.419
1989										
Transect with 1-ha Pino-Quercetum (forest island no. 3)										
Entomofauna	24	28	26	22	0.086	17	35	39	9	0.556
Diptera	25	26	25	24	0.039	18	28	34	20	0.283
Transect field – 1-ha birch-aspen woodlot (forest island no. 7)										
Entomofauna	24	26	27	23	0.086	23	28	36	13	0.373
Diptera	24	26	20	30	0.179	24	22	32	22	0.188

In the case of the Diptera, there were two times greater differences (values of the coefficient of variation) in colonization of the various ecotone transect zone between the transects including the large and small forest island (Table 3). This was mainly due to the tendency of the Diptera to cumulate more intensively in the field ecotone adjoining the large forest island.

Moreover, the transect including the 1-ha Pino-Quercetum forest island and the transect with the nearly 1-ha birch-aspen woodlot (both distant by ca. 1 km) were compared by insect colonization (Table 3); both forest islands were surrounded by winter barley cultures. The difference between transects in total

insect numbers was only 1%, and that in total insect biomass was ca. 5%. In this case the small difference in the size of the forest islands was unimportant, since – as earlier reported (Dąbrowska-Prost 1991) – the intensity of forest island colonization by insects is mainly related to the islands' size scale; in the present studies both forest islands belonged to the category of small islands.

According to the present results, the origin of the forest island exerts no substantial effect on insect distribution in the transects (Table 3). In both ecotones adjoining the Pino-Quercetum forest island there accumulated 54% of the total number of insects in the transect, and their biomass accounted for 74% of the total biomass; for the birch-aspen woodlot the respective values were 53% and 64% (Table 3). The values of the coefficient of variation point, however, to a much more uniform insect distribution in the transect with the birch-aspen woodlot, as compared with that including the Pino-Quercetum forest island (Table 3).

In general it can be stated that insects of the forest herb layer and brushwood layer tend to cumulate in the ecotones; this tendency is much more pronounced for the biomass than for numbers. The size of the forest island exerts no essential effect on the intensity of insect colonization of the ecotone zone. In the case of a different origin of the forest islands, young birch-aspen woodlots developing spontaneously on barrens form with crop field a habitat system which causes lower differentiation of insect numbers and biomass in the various zones of the system, as compared with the system formed by the 100 years old Pino-Quercetum forest island and crop field.

Studies of the occurrence of Diptera larvae in the transect with the 15-ha Pino-Quercetum forest island showed that the ecotone zone failed to be the most suitable habitat for the soil Diptera larvae; for this group of insects the forest ecosystem proved to be the main hatching site (Table 4). Only in late autumn and winter they occurred more abundantly in ecotone soil.

Table 4. Density (indiv. m⁻²) and biomass (mg w.w. m⁻²) of Diptera larvae along the ecotone transect with 13-ha Pino-Quercetum forest island and crop field during the autumnal increase in density (September–November 1988) and in the winter period (December 1988)

Parameters	21.09.	19.10.	9.11.	7.12.	\bar{x}
Density					
Forest	420	190	1650	990	562.5
Forest-field ecotone	40	120	330	380	217.5
Crop field (barley)	70	110	940	20	285.0
Biomass					
Forest	105.4	52.5	848.5	142.0	287.0
Forest-field ecotone	41.3	459.4	86.2	53.6	160.12
Crop field (barley)	24.0	111.2	67.5	0.2	50.75

3.2.2. Distribution pattern of the families, species and ecological groups of the Diptera

With the Diptera used as an example, it is possible to examine the differences between various ecological groups of insects in colonization of the zone of ecotones. The Diptera are very differentiated with respect to the habitat and trophic conditions, economic importance etc.; at the same time, they are mainly uniform with respect to many important features, e.g. the size and mobility of the mature forms, and the accessibility for definite types of predators. Moreover, they are a group dominant in the entomofauna of various types of landscapes and habitats, which reacts to varying living conditions mainly by changes in the community structure. On these grounds the Diptera may be regarded as an indicator group of insects, suitable for testing many ecological phenomena and processes, including those related to ecotones.

Similarly as in the case of many other animal groups, it is difficult to single out the Diptera families associated only with ecotone zones and families which avoid them completely. Most often there is a tendency for an either more intensive or less intensive colonization of the ecotones, as compared with the interiors of ecosystems. According to the present results, the following 4 types of the distribution pattern of the Diptera families in the ecotone transect could be distinguished (Fig. 2).

Type A involving evident preference for the ecotone zones could be exemplified by the distribution of the phytophagous Agromyzidae. A similar type of distribution was displayed also by the phytophagous beetles of the Curculionidae family, which were numerous in the analyzed material.

Type B associated with preference for the interior and margin zone of the forest ecosystem was characteristic of e.g. the predatory Diptera of the Empididae family and saprophagous Chironomidae. This type of spatial distribution was also shown by the Culicidae which, however, exhibited a much more evident affinity to the forest ecosystem interior than both above-mentioned families. All of these three families belong to insects associated with wet habitats and some – even with aquatic ones (larvae of certain Chironomidae species, Empididae and Culicidae).

Type C, opposite to the Type B, was represented by the Chloropidae family which predominantly includes phytophagous forms associated with cultivated plants or weed species. They inhabited mainly the crop field and its margin zone.

Type D more or less uniformly colonized all of the ecotone transect zones; it was represented by predatory Diptera of the Dolichopodidae family.

In the course of the 3-year studies, in the forest-field transect with the 1-ha Pino-Quercetum forest island there occurred 58 Diptera families among which 26% represented more or less distinctly the type A of spatial distribution, 29.5% – type B, 20.5% – type C and 24% – type D.

In the light of the above findings, only 1/4 of the Diptera families occurring in the terrain under study displayed a tendency for cumulation in the ecotone zone. In sum, however, in the 3 consecutive years of studies the greater number of families

occurred in this zone (Table 5). Four families during 3 years (in the consecutive years from 5 to 7 families) were associated exclusively with this type of habitat (Table 5). Values of the Koch dispersion coefficient (1957) expressing the degree of colonization of the habitats under study by different taxa, formulated as:

$$\frac{(T - s) : (n - 1)}{S} \cdot 100$$

where T – arithmetic sum of the number of taxa present in each test zone, S – no. of taxa occurring in the whole transect, n – no. of test zones (in this case n = 4), point to a clear-cut habitat selectivity of the Diptera families (only ca. 60% of the families occurred in all transect zones), that was fairly similar in the consecutive years of studies (Table 5).

Table 5. The number of Diptera families occurring in the different zones of the ecotone transect with 1-ha Pino-Quercetum forest island and crop field, and the degree of transect colonization by the families, measured by Koch dispersion index (1957)

In frames maximal number of families in the transect (3-year studies)

Zones	1988	1989	1991	1988– 1991	1988–1991		Evenness (Pielou 1966)	
	No. of Diptera families				Exclusive families			
Forest interior	37	32	36	44	3	8 4	0.667	
Forest ecotone	42	38	37	50	3		4	0.722
Field ecotone	35	37	41	47	0		4	0.792
Field interior	34	36	28	46	1			0.476
Koch dispersion coefficient, in %	63	62	62	74				

Shanon diversity index, modified by Pielou (1966) (H'/H°) and termed evenness index indicates that both ecotone habitats, as compared with the interiors of the forest and field ecosystems (Table 5), were characterized by particularly differentiated Diptera communities.

Likewise, the picture of the dominance structure of the Diptera in the ecotones showed that these communities were more diversified than those inhabiting the interiors of both ecosystems (Table 6). A substantial proportion of the biomass of the Diptera fauna (ca. 70%) in both ecotones was derived from 12–13 families, the biomass in the forest interior – from 6 families and that in the crop field interior – from only 4 families. A similar picture of the dominance structure in the different transect zones was obtained in the consecutive years of studies of the transects with the 1-ha Pino-Quercetum forest island, 35-ha forest island and birch-aspen woodlots.

The problem of the role of ecotones in preserving in the agricultural landscape some organisms beneficial or harmful to humans is of practical importance. According to Fig. 2, forest and field ecotones are colonized by phytophages, e.g. Agromyzi-

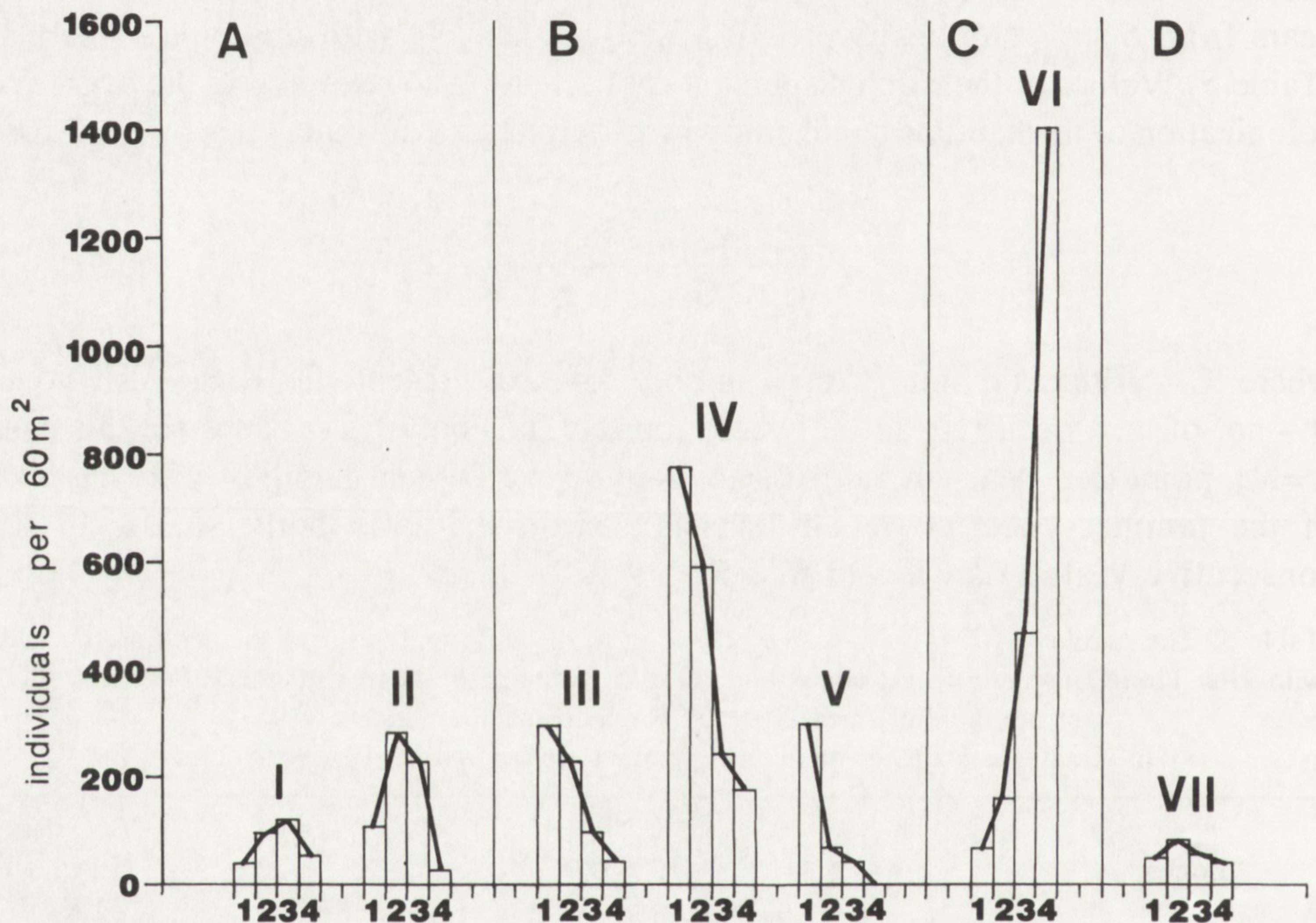


Fig. 2. Types of insect distribution along the transect:

interior of 1-ha Pino-Quercetum forest island (1), forest ecotone (2), field ecotone (3), crop field (4) (3-year studies)

I – Agromyzidae, II – Curculionidae, III – Empididae, IV – Chironomidae, V – Culicidae, VI – Chloropidae, VII – Dolichopodidae

dae and Curculionidae, forest ecotones – by predators (Empididae) and field ecotones – by Chloropidae which are important crop pests.

In general the preferences of the trophic groups of the Diptera for the ecotone transect zones are characterized by some regularities (Table 7). In the forest ecosystem and in both ecotones there is an evident dominance of the forms associated mainly with the decomposition of dead organic matter: saprophages and phyto-saprophages. The latter feed on both dead and living organic matter, but on the whole they create no economic hazard as crop pests. It is noteworthy that the percentages of both these trophic groups in the Diptera communities dropped successively from the forest through ecotones to the crop field. On the contrary, the percentage of the phytophages increased in the same succession (Table 7).

The quantitative relationships of the three trophic groups of the Diptera in the different transect zones testified to sharp dominance of one trophic group (saprophages) in forest interior (Table 7). In the forest and field ecotones the proportion of the phytophages evidently rose, but they were still ca. twice less numerous than the saprophages. In the crop field the phytophages were dominant.

Table 6. Dominance structure of the Diptera (in %) along the forest-field ecotone transect with 1-ha Pino-Quercetum forest island
In frames families being most numerous in the given habitat (3-year studies)

Families	Forest	Ecotones		Field	% in total transect
		forest	field		
1. Chironomidae	24	22	11	7	17
2. Dixidae	14	5			6
3. Culicidae	10				4
4. Empididae	9	8	4		6
5. Opomyzidae	9				4
6. Ptychopteridae	6	4			3
7. Chloropidae		5	21	54	19
8. Sciaridae		5	4		4
9. Ceratopogonidae		4		7	4
10. Anthomyiidae		4	7		4
11. Anthomyzidae		4	4		3
12. Agromyzidae		4	6		3
13. Phoridae		4			3
14. Sepsidae		3	4		2
15. Dolichopodidae		3			2
16. Sarcophagidae			4		1
17. Bibionidae			3		1
18. Drosophilidae				5	3
19. Syrphidae			2		2
Other families	28	25	30	27	9

Table 7. Trophic structure of the Diptera (in %) along the ecotone transect with 1-ha Pino-Quercetum forest island and crop field (3-year studies)

Trophic groups	Forest	Ecotones		Field	Total transect
		forest	field		
Phytophages	15	20	36	61	32
Saprophages and phyto-saprophages	73	65	53	33	57
Predators and parasites	12	15	11	6	11
Number relations between phytophages : saprophages + phyto-saprophages : predators + parasites	1 : 6 : 1	2 : 4 : 1	3 : 5 : 1	10 : 5 : 1	3 : 5 : 1

The reaction of the phytophages to ecotones could be exemplified by the Chloropidae which are one of the dominant Diptera families in the agricultural landscape (also in the terrain under study) (Table 6). As the main pests of agricultural cultures, they occurred in masses in the crop field (Table 8). As compared with the field, in

the field ecotone their numbers were three times lower, and in the forest ecotone – even ca. ten times lower (Table 8). Therefore, the interior of the field and its ecotone were the main habitats in which this group of the Diptera was cumulated. Forest ecotone constituted a clear-cut boundary of the Chloropidae occurrence (Table 8). This concerned both the forest ecotone adjacent to the Pino-Quercetum forest island and that adjoining the birch-aspen woodlot; in the latter case the Chloropidae penetrated in much greater numbers into both the field ecotone and forest ecotone (Table 9).

Table 8. Characteristics of the Chloropidae communities colonizing the zones of the ecotone transect with 1-ha Pino-Quercetum island (3-year studies)

Indices	Forest	Ecotones		Field	Total transect
		forest	field		
Distribution of numbers (%)	3	6	22	69	100.0
No. of species	12	20	25	17	33
Common species	11 (61%)		15 (68%)		6
	16 (73%)				
Exclusive species	1 (8%)	4 (20%)	3 (12%)	2 (11%)	–
	5 (27%)		9 (41%)		
Dominant species (%)	<i>Elachiptera tuberculifera</i> 22.5	<i>Oscinella frit</i> 18.5	<i>Oscinella frit</i> 35.0	<i>Oscinella frit</i> 71.0	<i>Oscinella frit</i> 58.0
Evenness index (Pielou 1966)	0.868	0.822	0.705	0.345	0.926
Similarity index (in %)	68.0		72.0		–
	70.0				

Table 9. Distribution of the Chloropidae (in % of their total numbers) along the ecotone transect with 1-ha Pino-Quercetum forest island and along the transect with 1.5-ha birch-aspen woodlot (1-year studies in 1988)

Transect	Forest	Ecotones		Field
		forest	field	
With Pino-Quercetum forest	2	6	9	83
With birch-aspen woodlot	5	14	20	61

Chloropidae communities in the ecotones, as compared with those in the field and forest, were richer in species (as indicated by the evenness index calculated as the ratio H'/H° – Pielou 1966) and at the same time were more specific (greater number of exclusive species) (Table 8). The similarity of the Chloropidae species community in the field ecotone and field interior exceeded the analogous in similarity the forest ecotone and forest (Sørensen similarity index

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

where a – no. of species in habitat A, b – no. of species in habitat B, c – no. of common species) (Table 8).

As some factors (e.g. the origin and size of the forest islands under study) exert a relatively slight effect on the distribution and qualitative structure of the insect communities in the ecotone, it is possible to propose a general pattern of ecotone distribution of the entomofauna, which would emphasize the main characteristic features of this distribution.

It was found that so prepared the data confirmed the earlier detailed conclusions concerning the quantitative and qualitative distribution of the entomofauna in the transect, which testified to a particular preference of this group of animals for the ecotones where ca. 55% of the numbers of the entomofauna and ca. 70% of its biomass were cumulated. Diptera colonized the transects much more uniformly than the total entomofauna, as indicated by the ca. two times smaller value of the coefficients of variation (Table 10). Individuals occurring in the ecotones, as compared with those present in the interiors of the forest and field ecosystems, were 1.5–2.5 times heavier (Table 10).

Ecotones, as compared with the ecosystems of the forest and field, were colonized by more diverse Diptera communities; this was due to the local occurrence of a greater total number of families, as well as to a more flattened dominance structure (greater pool of families in the group of dominants). At the same time, the ecotones displayed the pressure of many so-called "sporadic" families (occurring in this type of habitat as single individuals) and by the presence of very few families characteristic of only this type of habitat (Table 10).

A similar analysis of the general pattern of ecotone distribution, prepared for the mainly phytophagous Chloropidae family being dominant among the Diptera, testified to the great importance of the field ecotone and to some degree also of the forest ecotone for spreading and preservation of this Diptera group in the agricultural landscape (Table 11).

3.3. NUMBERS AND BIOMASS CHANGES, AND SPECIES (FAMILIES) MIGRATION ACROSS THE ECOTONE

3.3.1. Seasonal changes in entomofauna flux between forest islands and fields

Studies of the seasonal changes in entomofauna occurrence in ecotone transects indicated that in early spring (April) when in crop fields plants only begin to sprout, the forest is the main habitat for the entomofauna (Fig. 3).

With a lapse of time (May, June) and with the appearance of a fairly high and dense plant cover in the fields, the insects which in this period emerge in masses begin to occur in all of the ecotone transect zones. However, the interior of the forest island still continues to be the optimal habitat for insects, and both ecotones are much more suitable than the crop field interior. In July in the field the phytophages

Table 10. General pattern of entomofauna distribution in the ecotone transect.

Total data for 4 transects with mixed forest (3-year studies of the transect with forest island no. 3 and 1-year studies of the transect with forest islands no. 1) and for 2 transects with birch-aspen woodlots (1-year studies of forest islands nos 5 and 7)

	Forest	Ecotones		Field	Coefficient of variation	Total transect
		forest	field			
Distribution of numbers (%)						
Entomofauna	28	31	25	16	0.352	100%
Diptera	25	34	22	19	0.258	100%
Distribution of biomass (%)						
Entomofauna	24	33	35	8	0.607	100%
Diptera	24	35	27	14	0.339	100%
Mean individual weight						
Entomofauna	1.514	2.268	2.761	1.047	—	—
Diptera	1.080	1.170	1.430	0.833	—	—
No. of Diptera families	52	55	52	49	—	58
No. of sporadic families	4	8	7	3	—	2
	1	1	0	0		
No. of exclusive families		4		2	—	—
			1			
No. of Diptera families accounting for 55% community numbers	Chironomidae Culicidae Empididae	Chironomidae Empididae Ceratopogonidae Culicidae Agromyzidae Sciaridae	Chironomidae Chloropidae Anthomyiidae Drosophilidae Ceratopogonidae Agromyzidae Sphaeroceridae Dolichopodidae	Chloropidae Drosophilidae	—	Chironomidae Chloropidae Culicidae Ceratopogonidae Empididae Drosophilidae
Evenness index (Pielou 1966)	0.647	0.776	0.802	0.609	—	0.755

Table 11. Species structure of the Chloropidae

Total data for 4 transects with mixed forest (3-year studies of the transect with forest island no. 3 and 1-year studies of the transect with forest island no. 1) and for 2 transects with birch-aspen woodlots (1-year studies of forest islands nos 5 and 7)

Indices	Forest	Ecotones		Field	Total transect
		forest	field		
Distribution of numbers in the transect (%)	2	6	28	62	100.0
No. of species	18	24	32	21	39
Common species	16 (62%)		20 (61%)		9 (23%)
	19 (52%)				
Exclusive species	1	2	6	1	
	6 (23%)		12 (36%)		-
	9 (24%)				
Dominant species in numbers (%)	<i>Elachiptera tuberculifera</i>	<i>Oscinella frit</i>	<i>Oscinella frit</i>	<i>Oscinella frit</i>	<i>Oscinella frit</i>
	22	25	27	80	56
No. of sporadic species	6	6	5	2	-
Evenness index	0.83	0.86	0.67	0.37	0.50
Similarity index (in %)	34		48		-
	38				

(e.g. Chloropidae) occur in masses, and in this period the distribution of the numbers and biomass of insects in the transect is very equalized, as shown by the values of the coefficients of variation (Table 3).

In August harvest begins and is followed by ploughing, this resulting in insect retreating from the crop fields. From August until October the ecotones become the main insect habitat, in which individuals and biomass cumulate; at the end of the vegetation season (November) the forest ecotone and forest interior are the only insect occurrence sites (Fig. 3).

In 1991, during sample collection, unexpectedly in a field adjacent to the forest island ploughing was performed, and thus the changes in insect dispersion, resulting from elimination of the field habitat, could be observed (Fig. 4). It was found that at this time the insects moved from the field mainly to the ecotone zone, in particular to the field ecotone. After restoration of the culture, the insects recolonized the whole transect; the values of the coefficient of variation pointed to a ca. two fold increase in the uniformity of the terrain colonization by insects (Fig. 3).

The importance of the ecotones for various insect groups is differentiated. The course of the seasonal translocations of the Diptera families with different preferences for the ecotone zones indicated that in general the distribution type of these groups persisted throughout the whole vegetation season, and only the

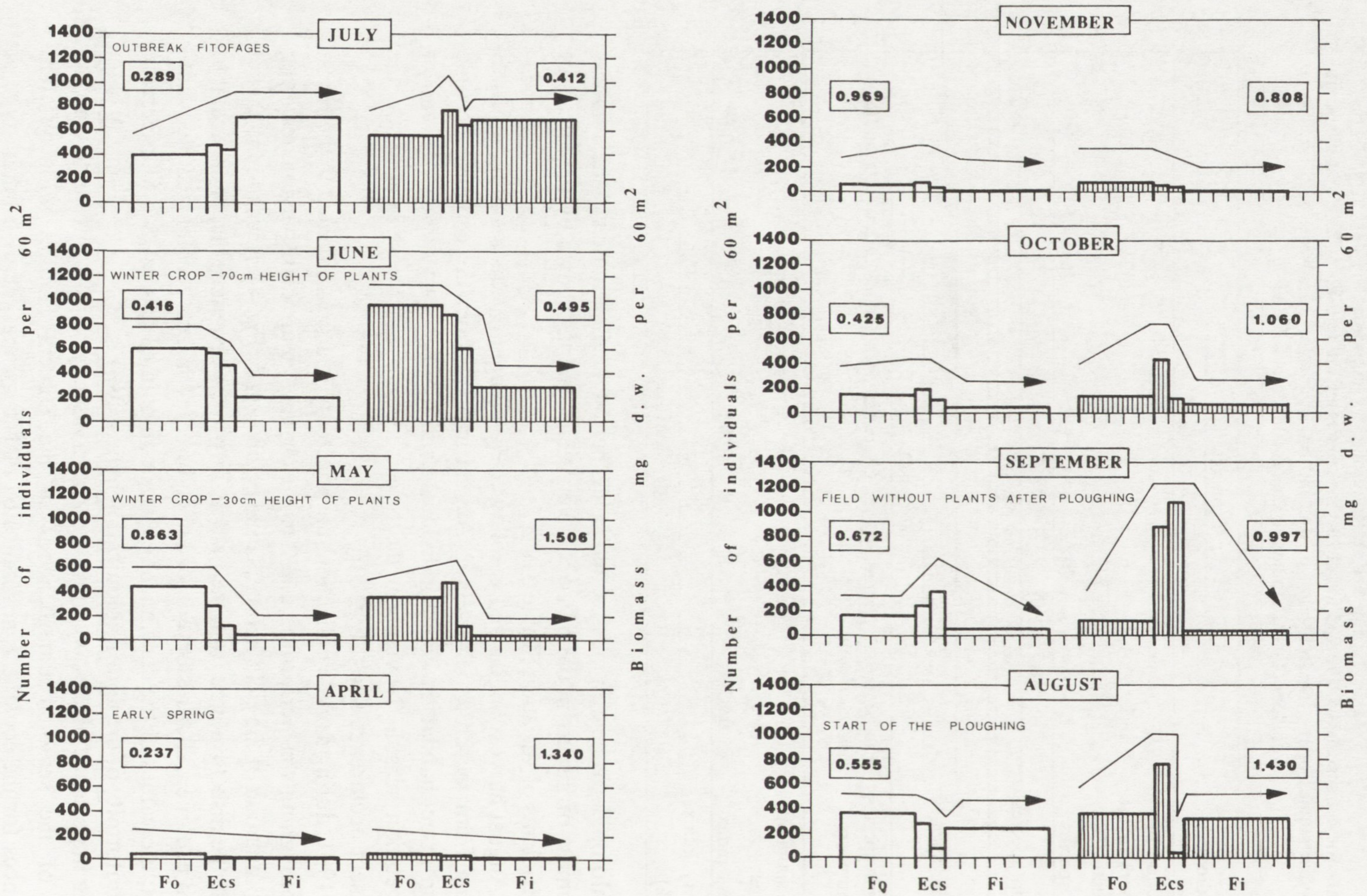


Fig. 3. Seasonal dynamics of the entomofauna (density and biomass per m²) in ecotone transect with 1-ha Pino-Quercetum forest island (no. 3) in 1988
 In frames - values of the coefficient of variation (Fo - forest, Ecs - ecotones, Fi - field)

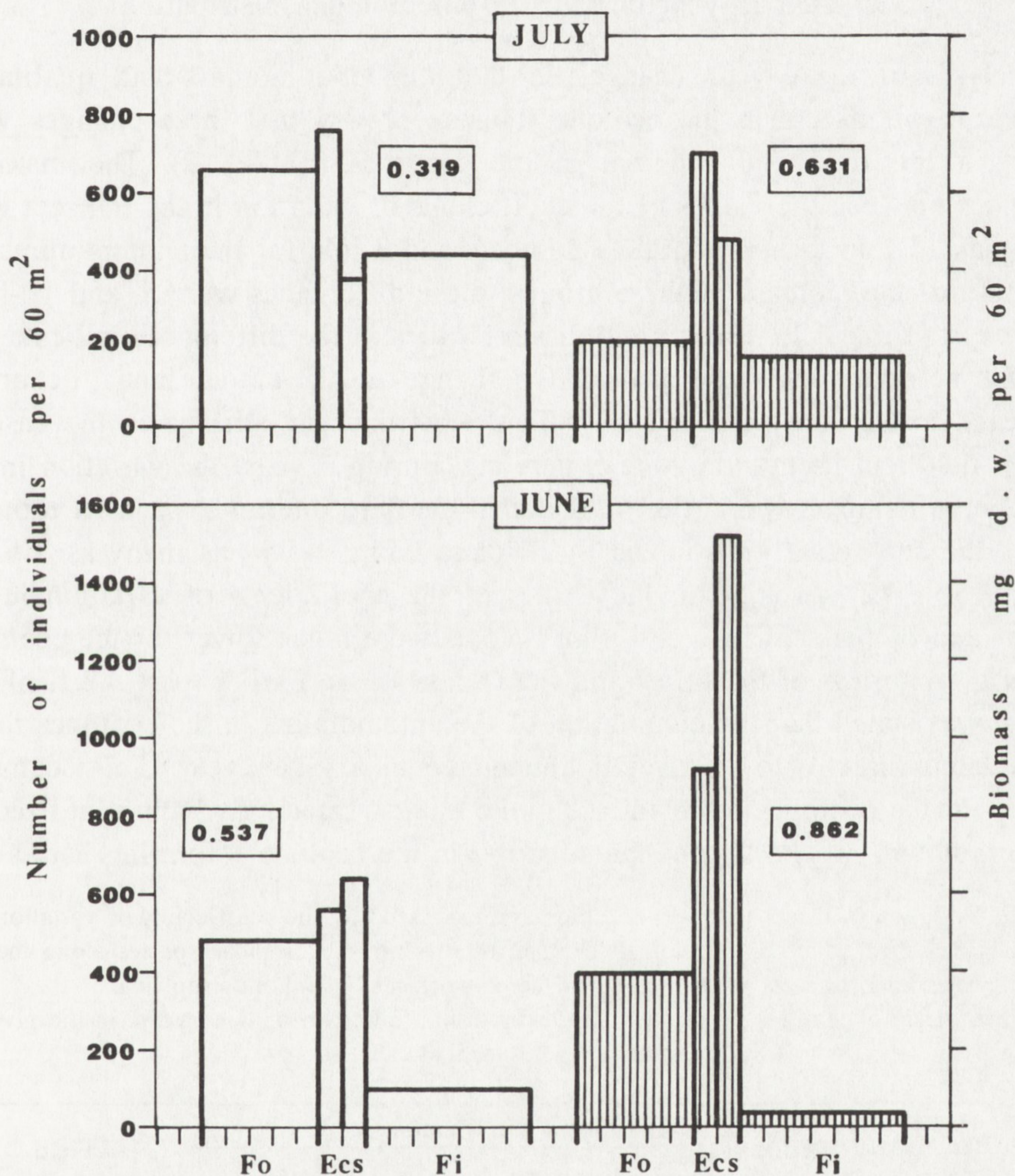


Fig. 4. The effect of ploughing (in July) on spatial distribution of the entomofauna density and biomass in ecotone transect with 35-ha Pino-Quercetum forest island (no. 1) in 1991

In frames – values of the coefficient of variation

(Fo – forest, Ecs – ecotones, Fi – field)

intensity of colonization of the different zones, including the ecotones, underwent some changes.

For many insect groups, even for those which show no preference for the ecotone habitats, the ecotones are specially important in early spring. This may be due to the fact that in this period in the ecotones the microclimatic and trophic conditions are usually preferable; for example, the predators and phytophages find there a more abundant trophic base and more suitable habitat conditions (Dąbrowska-Prot 1991, Wójcik 1991, Wójcik and Wasilowska 1995).

Ecotones, as compared with the ecosystem interiors, displayed a greater qualitative diversity of the Diptera structure (Tables 5, 6, 8, 10). At the same time their Diptera structure was more stable, as confirmed by the high proportion of the Diptera families occurring there during the whole 3-year period of studies (Table 12). On the other hand, in all of the transect zones, and particularly in the ecotones, among the Chloropidae communities the species occurring in only 1 year were dominant (Table 12). This testifying to a generally high variability of this community in the consecutive years of studies, particularly in the ecotones where the proportion of the species occurring during all 3 years of studies was by ca. 10% lower than in the interiors of the forest and field ecosystems.

The importance of the ecotone for the Diptera may vary in dependence on the effect of different factors. For example, Melničenko (1949) has reported that in autumn the Chloropidae species migrated from crop fields to the margin parts of the mid-field woodlots, which are their wintering sites. In turn, Lewis (1969, 1970) has described the role of wind in the cumulation of the Diptera under the cover of woodlots. The climatic conditions of a given year are of great importance. This could be exemplified by the mosquitoes which are specially sensitive to weather conditions (Fig. 5). According to Dąbrowska-Prot et al. (1973), in a dry year (high temperature, low humidity) the mosquitoes were mainly present in the forest ecosystem, whereas only inactive individuals occurring in the forest herb layer and brushwood layer appeared in the forest and woodland meadow ecotone in greater

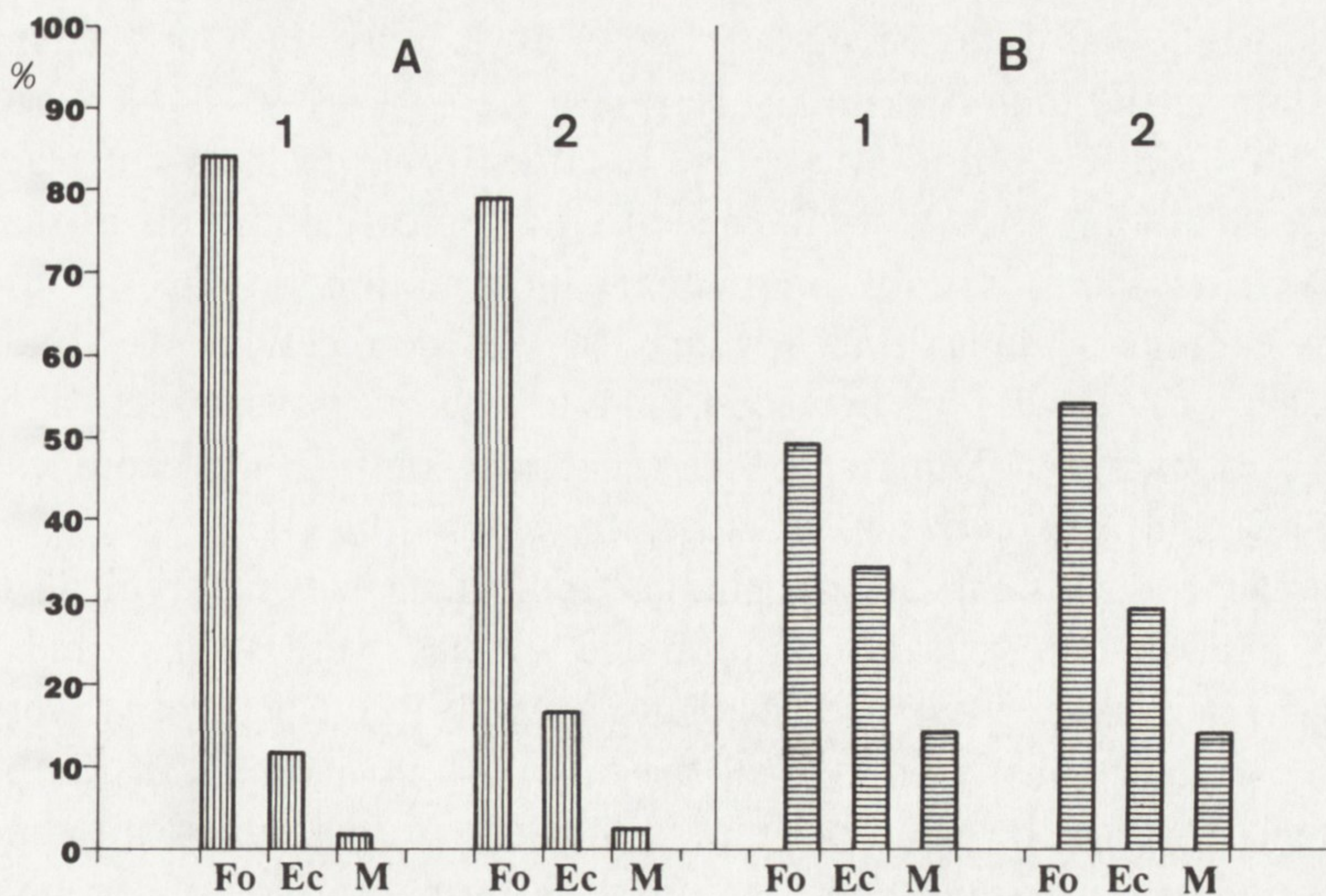


Fig. 5. Distribution of the numbers (%) of: 1 – active Culicidae (individuals flying in the forest herb and shrub layers); 2 – inactive Culicidae (sitting in vegetation) in ecotone transect with alder forest, ecotone and natural meadow, in: A – a dry and hot year (climatic conditions adverse for mosquitoes) and B – a wet and warm year (favourable climatic conditions) (Dąbrowska-Prot et al. 1973, modified) (Fo – forest, Ecs – ecotones, M – meadow)

numbers. In a wet year, both the mosquitoes actively moving in the habitat and the inactive ones colonized much more uniformly the whole transect, including the open terrain (woodland meadow) adjacent to the forest and ecotone. In a wet year, as compared with a dry one, the percentage of the mosquitoes colonizing the ecotone was twice higher. Under optimal climatic conditions the ecotone was an appropriate habitat for the mosquitoes, and consequently a qualitatively and quantitatively rich community was formed there. Moreover, at this time the ecotone was a transit zone for mosquitoes in their flights from the forest to the adjoining open terrains. In the years with adverse weather conditions, the ecotone was a clear-cut boundary of mosquito occurrence, and the adjacent open terrains were almost completely eliminated as a mosquito habitat (Dąbrowska-Prot et al. 1973, Dąbrowska-Prot and Łuczak 1968).

4. DISCUSSION

The present investigations are a continuation of the studies on the role of forest islands in fauna shaping in the agricultural landscape. Earlier it has been found that the margin zone of small forest islands may account for up to 24% of their surface and be decisive of the intensity of the biological material exchange with the surrounding open terrains (Dąbrowska-Prot 1991). With a rise in landscape mosaic, the ecotones play an increasingly important role in the landscape structure and functioning because of an increase in both – their number and proportion in the total area of the terrain.

In the literature there are only sparse data testifying to clear-cut reactions of invertebrates, including insects, to the specific ecological conditions of the contact zone, as well as there is only fragmentary information on the occurrence of exclusively ecotone – inhabiting species. In this connection, the findings by Michalska (1970) who has revealed among phytophagous insects as many as 8 butterfly species and 4 Diptera species occurring only in the ecotones formed between forest and open terrains, are specially noteworthy.

The present results of 3-year studies indicated that the typical ecotone-inhabiting Diptera families and Chloropidae species were scanty, and that the Araneae did not include these species (Łuczak 1995). Such cases were scarce among insects; they usually concerned the taxa low in numbers in the period of studies. Thus, it cannot be ruled out that in the case of their abundant appearance, their dispersion in the terrain would be more uniform and would also involve the interiors of ecosystems. In this connection only the taxa with a clear-cut preference for the margin zones of ecosystems and the taxa evidently avoiding them could be singled out for certain (Fig. 2).

Undoubtedly, the ecotones preserve a high level of biological diversity in the landscape. This is due both to the usually higher number of the taxa occurring in this

zone (Tables 5, 8, 10, 11) and to the greater number of the taxa forming the group of dominant species (slightly expressed dominance structure) (Tables 6, 10). At the same time the forest interior and forest ecotone, as compared with the field and its ecotone, are colonized by more differentiated Diptera communities (Table 10).

From the standpoint of fauna biodiversity, its specificity in the different transect zones is of importance; this biodiversity can be assessed from the proportion of the common taxa and of the taxa occurring exclusively in a given zone. According to the present results, the forest and its ecotone zone, as compared with the habitat system: crop field and its ecotone, are colonized by more characteristic Diptera communities which at the same time are alike (Tables 5, 10). The ecotone zone was colonized by the fauna of low specificity, despite the greater differentiation of the Diptera than that found for the interiors of the forest and field (this differentiation was due, among others, to more frequent occurrence of the so-called "sporadic" families in the ecotones (Table 10).

Vice versa, in the case of the Chloropidae family belonging among the Diptera associated mainly with strongly synantrophized habitats and crop-field habitats, the field and its ecotone were characterized by a greater number of common species and of those occurring exclusively in these habitats (Tables 8, 11).

Similarly as in the case of the whole Diptera group, the ecotone zone, as compared with the interiors of the ecosystems, was colonized by much more differentiated Chloropidae communities which at the same time were fairly specific (Tables 8, 11); this failed to become manifest for a taxon as big as the Diptera. The habitat conditions of ecotones, as compared with ecosystem interiors, allow for penetration and persistence of a greater number of species, particularly in the periods of drastic seasonal changes in crop field vegetation.

In contrast to the forest ecotone, the problem of differentiation of the crop field margin zone has always been controversial and was considered but seldom in field studies. For example, Kromp and Steinberg (1992) have investigated the qualitative structure of the predatory Arthropoda occurring in the grassy margin zone and interior of a wheat crop field; they found that both zones were colonized by one Carabidae community moving actively between them. Spiders have been found to form two different communities; the community of field interior was characterized by a small number of species and clearly expressed dominance structure, and the community of the field margin part included many species low in numbers. There is a striking analogy with the structure of the Diptera communities in crop fields and their ecotones, as found in the present studies. Kromp and Steinberg (1992) have concluded that the crop field margin zones may serve as refuge habitats for the predators which are potential regulators of the numbers of crop pests.

Dennis and Fray (1992) have analyzed the role of the crop field margin zones as wintering sites for the predatory Arthropoda (particularly aphidophages and the role of these zones in enhancing the Arthropoda species diversity. Lagerlöf et al. (1992) have stressed the importance of field margins in

preserving the qualitative and quantitative richness of pollinating insects (Diptera, Hymenoptera, butterflies and others).

All of these observations refer to the phenomenon of preserving by the different ecotone transect zones an animal community of a definite trophic structure, this being important on economic grounds. According to the present results, the trophic structure of the Diptera communities in forest interior and forest ecotone was more similar than this structure in crop field and field ecotone (Table 7). In the habitat system: forest–forest ecotone, the forms associated with decomposition of dead organic matter were clearly dominant, whereas the phytophages, predators and parasites were much less abundant.

In the field ecotone, similarly as in forest habitats, the saprophages were dominant, whereas the phytophages were twice less numerous. In the crop field interior the proportion of both above mentioned trophic groups in the Diptera communities was opposite than that in the field ecotone (Table 7).

As a result the proportion of the plant phytophagous pests in the Diptera communities increased from forest interior through the ecotone zone to crop field interior, and that of the other trophic groups dropped in the same succession.

The present 3-year studies testify to a clear-cut cumulation of insects (numbers and biomass) in the ecotone zone (Tables 2, 3, 10). It may thus be assumed that an increase in the number and length of the ecotones of the forest–field type raises the quantitative level of the entomofauna in the landscape. A similar phenomenon has been recorded by Goszczyński (1985) for populations of some predatory mammals (foxes, badgers) and birds (buzzards), the numbers of which depended on the length of the forest–field boundary. These were eurytopic species, for which the ecotone zone was a reproduction and refuge site, and the adjacent fields – a feeding ground.

It is of interest that the 3-year fluctuations in entomofauna numbers and biomass in the ecotones were many times smaller than those in the interiors of the forest and crop field (Table 12). This testifies to a certain independence of the quantitative changes in the ecotone entomofauna with respect to alterations in the ecotone-forming ecosystems.

The role played by the ecotones varies in the course of the vegetation season (Fig. 3) and is specially important in the case of agrotechnical treatments in crop fields (Fig. 4). At these times the ecotones act as refuge habitats for the insects migrating from crop fields.

Likewise, the climatic conditions are an important environmental factor decisive of the significance of ecotones for insects. For example, in the case of the Diptera groups particularly sensitive to weather conditions (e.g. mosquitoes), in the years with adverse climatic conditions the ecotones represent a habitat boundary for their migration into open terrains, whereas in the years with favourable weather the ecotones constitute a transition zone in their migrations between forest and adjoining open terrains (Fig. 5).

In general, the forest-crop-field ecotones are for the entomofauna a multizone habitat owing to the differentiation of the margin zones of the forest and field. The ecotones promote the overall qualitative and quantitative richness of the entomofauna in the landscape. They are colonized by specific insect communities which differ from the communities inhabiting the interiors of the ecosystems in the number of taxa, dominance and trophy structure, as well as in seasonal and many years' dynamics. Their "permeability" to insects is related both to the ecological characteristics of the taxa and preferences for margin zones, as well as to the environmental conditions prevailing in different periods of the vegetation season and in consecutive years.

Therefore, the intensity of the exchange of insect species, number and biomass between ecosystems depends, on the one hand, on the ecological properties of the insect organism and, on the other, on the environmental conditions conceived in a broad sense. Thus the ecotones, together with other elements of the landscape structure, are decisive of landscape functioning, intensity of the biological material exchange between ecosystems (habitats) and qualitative richness of the local fauna.

5. SUMMARY

Remainders of old mixed forests (Pino-Quercetum) and birch-aspen woodlots developing spontaneously on barrens are a dominant natural element of the agricultural landscape of the Masurian Lakeland. Both above types of forest islands, adjacent crop fields and their ecotones were the terrain of the present environmental, phytosociological and biocoenotic studies (Fig. 1).

It was found that the margin parts of forest and fields differ in the microclimatic conditions (Table 1), vegetation composition and density from the forest and field interiors as well as differ between each other. Thus, a two-zone structure of the ecotones was assumed in these studies, and their width was accepted on the basis of phytosociological records.

Insects (including the Diptera) of the forest herb and brushwood layers displayed a tendency for accumulation in the ecotones; this was more evident in the analyses of the spatial distribution of their biomass than in that of their numbers (Table 2).

The size of forest island exerts no essential effect on the intensity of ecotone colonization by insects, whereas the forest island origin is of significant importance. All around the old, equilibrated Pino-Quercetum forest associations there is formation of ecotones colonized by a much richer entomofauna than that occurring in the interiors of forest and crop field (Tables 3, 5). It is noteworthy that the quantitative level of the ecotone fauna is not related directly to fauna abundance in the forest and field habitats. This testifies to a certain autonomy of the ecotones in relation to the habitats which form them.

Several types of the Diptera families distribution pattern were found to occur in ecotone transects (Fig. 2). Among 58 Diptera families, 26% preferred the ecotones (e.g. Agromyzidae), 29.5% – the interior and margin zone of the forest ecosystem (e.g. Empididae, Chironomidae, Culicidae), 20.5% – the crop field and its margin zone (e.g. Chloropidae), and 24% preferred to the same extent all of the ecotone transect zones (e.g. Dolichopodidae). Thus, 1/4 of the Diptera families colonized mainly the ecotone zone.

Ecotones were inhabited by Diptera communities being very variable from year to year (Table 12) and at the same time very differentiated in family composition (Tables 6, 7, 8). This

was due to the occurrence of a greater number of families in the ecotones, as compared with other transect zones, as well as to the relative richness expressed by an equalized dominance structure and frequent appearance of the so-called "sporadic" families. On the other hand, there were only few families characteristic of only this type of habitat (Tables 10, 11).

Because of the habitat preferences of the Diptera trophic groups, in the forest island interior and in both ecotones the forms associated with dead organic matter decomposition were most numerous (Table 7). Although the proportion of phytophages in the ecotones increased, they were still ca. 2 times less numerous than the saprophages. In crop fields the phytophages were dominant.

The entomofauna migrated seasonally between the ecotone transect zones (Fig. 3). In the course of field ploughing the insects migrated in masses to the field ecotone, and less intensively to the forest ecotone (Fig. 4).

The importance of the ecotone for the entomofauna as a refuge habitat changes in dependence on the climatic conditions (Fig. 5), period of the vegetation season and intensity of agrotechnical treatments in crop fields, but it is a habitat always colonized by numerous and diversified Diptera communities. At the same time it is a zone of fauna exchange between the forest and field ecosystems.

6. POLISH SUMMARY

Dominującym, naturalnym elementem krajobrazu rolniczego Pojezierza Mazurskiego są resztki starych lasów mieszanych (Pino-Quercetum) oraz samorzutnie rozwijające się na nieużytkach zadrzewienia brzożowo-osikowe. Oba typy wysp leśnych, przyległe do nich pola uprawne oraz ich ekotony były terenem badań środowiskowych, fitosocjologicznych i biocenotycznych (rys. 1).

Stwierdzono, że brzeżne partie lasu i pola różnią się warunkami mikroklimatycznymi (tabela 1) oraz składem i zagęszczeniem roślinności, zarówno od wnętrza pola i lasu, a także między sobą, dlatego w badaniach uwzględniono dwustrefową strukturę ekotonów, a ich szerokość ustalono na podstawie zdjęć fitosocjologicznych.

Owady, w tym Diptera warstwy runa i podszytu wykazywały tendencję do skupiania się na ekotonach, co wyraźniej ujawnia się w analizach rozkładu przestrzennego ich biomasy, niż liczebności (tabela 2).

Wielkość wyspy leśnej nie wywiera znaczącego wpływu na intensywność zasiedlania przez owady ekotonów, natomiast jej pochodzenie ma tu istotne znaczenie. Wokół starego, zrównoważonego zbiorowiska leśnego typu Pino-Quercetum wytwarzają się ekotony zasiedlane przez entomofaunę znacznie bogatszą niż we wnętrzu lasu i na polu uprawnym (tabele 3 i 5). Godnym uwagi jest fakt, że poziom ilościowy fauny na ekotonach nie był bezpośrednio uzależniony od jej obfitości w środowisku leśnym i polnym. Wskazuje to na pewną ekologiczną autonomię ekotonów w stosunku do środowisk je tworzących.

Wykazano istnienie kilku typów rozmieszczenia rodzin muchówek na transektach ekotonowych (rys. 2). Z 58 rodzin Diptera 26% preferowało ekotony (np. Agromyzidae), 29,5% – wnętrze ekosystemu leśnego i jego strefę brzeżną (np. Empididae, Chironomidae, Culicidae), 20,5% – pole uprawne i jego strefę brzeżną (np. Chloropidae), 24% – w równym stopniu wszystkie strefy transektu ekotonowego (np. Dolichopodidae). Tak więc 1/4 rodzin Diptera zasiedlała głównie strefę ekotonów.

Ekotony zasiedlane były przez bardzo zmienne z roku na rok (tabela 12), ale jednocześnie bardzo zróżnicowane jakościowo, zespoły Diptera (tabele 6, 7 i 8). Wynikało to zarówno z faktu występowania tam zwykle większej, niż w innych strefach transektu, liczby rodzin, jak i względnego bogactwa wyrażającego się dość wyrównaną strukturą dominacyjną oraz częstego pojawiania się rodzin tzw. sporadycznych. Natomiast występowało tam mało rodzin charakterystycznych tylko dla tego typu środowiska (tabele 10 i 11).

Preferencje środowiskowe grup troficznych Diptera powodowały, że we wnętrzu wyspy leśnej i w obu ekotonach najliczniejsze były formy związane z rozkładem martwej materii organicznej

(tabela 7). W ekotonach wzrastał wprawdzie udział fitofagów, ale były tam one ciągle jeszcze około 2-krotnie mniej liczne niż saprofagi. Na polach uprawnych dominowały fitofagi.

Stwierdzono sezonowe przemieszczanie się entomofauny między strefami transektu ekotonowego (rys. 3). Szczególnie intensywne było zjawisko masowego wycofywania się owadów na ekoton polny, a słabiej na ekoton leśny w czasie trwania na polu orki (rys. 4).

Znaczenie ekotonu dla entomofauny jako schronienia ulega zmianie w zależności od warunków klimatycznych (rys. 5), okresu sezonu oraz intensywności zabiegów agrotechnicznych na polach uprawnych, ale zawsze jest to środowisko zasiedlane przez liczne i różnorodne zespoły Diptera. Jest to jednocześnie strefa wymiany fauny między środowiskami leśnymi i terenem pól uprawnych.

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