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SOIL-LITTER MACROFAUNA IN THE MIXED FOREST AND MIDFIELD SHELTERBELTS OF DIFFERENT AGE (TUREW AREA, WEST POLAND)

ABSTRACT: The paper deals with the composition, density and biomass of soil-litter macrofauna in four midfield shelterbelts of different age and, comparatively, in the neighbouring mixed forest.

The increase was observed along with the shelterbelt ageing of: 1) numbers of all macrofauna and particularly of some taxa (Symphyla, Chilopoda, coleopteran larvae and imagines and some dipteran larvae), 2) biomass of all macrofauna, of soil fauna (Group I) and of coleopteran larvae, 3) share of zoophages in all macrofauna and in dipteran larvae, 4) share of phytophages in coleopteran larvae communities, 5) average individual biomass, 6) taxonomic richness and the biodiversity (H'), 7) similarity of composition and domination structure of all macrofauna and of dipteran larvae to those in forest communities. The decrease of density of dipteran larvae, particularly of Chironomidae and Sciaridae and the share of saprophages in all macrofauna and in dipteran larvae was also observed.

Successional stages of more numerous invertebrate taxa in newly established woodlots are described. Dipteran larvae were the pioneers in colonising newly established shelterbelts, particularly larvae from two families: Chironomidae and Sciaridae. Their combined contribution to the total density of dipteran larvae was 92%.

KEY WORDS: shelterbelts, mixed forest, soil-litter macrofauna, density, biomass, individual biomass, domination structure, trophic structure, succession

1. INTRODUCTION

Midfield shelterbelts introduced in West Poland (Turew area, near Poznań) in the XIX century by General Dezydery Chłapowski were the subject of many studies, which described various roles they played in agricultural landscape. Apart from their purely mechanical functions (wind shelter, soil erosion, shadowing etc.) the shelterbelts are a habitat for organisms, for which they play a role of refuges and ecological corridors thus maintaining and enriching biodiversity of croplands (Boudry 1988, Thomas *et al.* 1994, Karg 1995, Karg and Ryszkowski 1996, Wratten 1998, Paoletti 2001, Olechowicz 2004).

Equally important, apart from the effect of shelterbelts on adjacent fields, are changes taking place within the shelterbelt itself during its development and the sequence of colonization of this new

ecosystem by the organisms. New plantings of midfield shelterbelts that started in the agricultural landscape of Turew area in 1993 (Kujawa and Karg 1998) enabled to follow this process. Intensive studies of epigeic fauna have been carried out in the shelterbelts (Karg 1995, 1998, Karg and Ryszkowski 1996, Ryszkowski *et al.* 2001). The studies on soil-litter macrofauna are necessary to evaluate the process of shelterbelts colonization and their development. Soil animals are known to be a good indicator of the environmental changes (Vanek 1959, van der Drift 1967, Wallwork 1970, Szujecki *et al.* 1977, Olechowicz 1986, 1995, 1998, 2004, Schaefer and Schauermann 1990, Stork and Eggleton 1992, Frouz 1994, 2001, Paquin and Coderre 1997, Paoletti 2001).

2. STUDY SITES, MATERIAL AND METHODS

The studies were carried out in the Turew area, near Poznań (West Poland) in 1999 and 2000 in the following woods (abbreviated denotation is given in brackets):

– Mixed forest (Forest) of an area of 77 ha with tree stands different in species and age (the oldest trees were over 120 years old). Main species were: Scotch pine (*Pinus silvestris*) (80% of trees), common oak (*Quercus robur*) (20%) with the admixtures of common birch (*Betula verrucosa*), larch (*Larix decidua*) and black locust (*Robinia pseudoacacia*).
– 150 years old shertelbelt (S 150). Tree stand is composed mainly of black locust (*Robinia pseudoacacia*) and of the oak (*Quercus robur*) and linden (*Tilia cordata*) being a supplement of the damaged stands.
– 6–7 years old shertelbelt (local name: “Wyskoć”) (S 6–7) planted in December 1993; 340 m long and 17.5 m wide strip of an area of 5980 m^2. Thirteen tree species are planted there in 11 rows. The number of trees and shrubs is 3400.
– 3–4 years old shelterbelt (local name: “Rogaczewo”) (S 3–4) planted in October 1996; 1650 m long and 15 m wide strip of an area of 24750 m^2. Twenty one tree and shrub species in the total number of 8860 are planted in 4 to 10 rows.
– 1–2 years old shelterbelt (local name: “Wyskoć C”) (S 1–2) planted in October 1998; 800 m long and 12 m wide strip of an area of 9600 m^2. Fifteen tree species and 3 shrub species are planted in 7 rows.

All studied shelterbelts have a characteristic north-south direction of strips. Basic data on soil and litter of studied shelterbelts are given in Table 1.

Ten soil samples of an area of 100 cm^2 and 15 cm thick were taken once from the above woods. Sampling occassions and numbers of collected samples are given in Table 2. Animals were extracted from soil by the Tullgren’s method modified by Kempson *et al.* (1963). Agitation of animals lasted 10 days until total drying of the soil. Picric acid was used to preserve animals.

Table 1. Organic carbon and nitrogen content and pH of soil and litter in shelterbelts of different age (Kostro-Chomać 2003).

age of shelterbelts	150 years		6–7 years		3–4 years		1–2 years	
	soil	litter	soil	litter	soil	litter	soil	litter
pH (KCl)	3.7	5.1	4.3	5.1	6.2	6.1	5.4	7.3
pH (H_2O)	3.9	5.1	4.7	6.0	6.4	6.3	5.8	6.6
C (%)	2.4	21.5	0.6	20.8	0.6	16.2	0.5	18.1
N (%)	0.19	1.27	0.06	0.99	0.06	0.90	0.05	1.03
C:N	12	17	9	21	12	18	10	17

Table 2. Sampling time and number of soil samples collected in the mixed forest and shelterbelts (S) of different age (in years).

Woods	Oct.1999	Apr.2000	June 2000	Sept.2000	Number of samples
Forest	–	–	+	+	20
S (150)	–	+	+	+	30
S (6–7)	+	+	+	+	30
S (3–4)	+	+	+	+	40
S (1–2)	+	+	+	+	40

Biomass of communities was calculated as a product of density and mean values of individual weight within a given size class of particular taxa. Before weighting the animals were dried at 85°C.

Statistical data processing involved:

- non-parametric analysis of variance – the Kruskall-Wallis test,
- a comparison of two samples with the Student's t-test,
- Shannon and Weaver's index of biodiversity (H'),
- indices of similarity of animal communities:

1) after Marczewski and Steinhaus (1959) to compare composition of communities:

$$s = w/(a+b-w) \quad (1)$$

and 2) after Romaniszyn's modification (1970) to compare domination structure:

$$S = 100C/200-C, \quad (2)$$

where:

s, *S* – similarity of the two compared communities,
a – the number of taxa in community A,
b – the number of taxa in community B,
w – the number of taxa common for A and B,
C – sum of lower percentage shares of particular taxon of the two compared communities.

Studied soil-litter invertebrate animals according to van der Drift (1951) can be classified as macrofauna (size 2–20 mm). Two groups were distinguished among these animals:

- Group I – soil animals closely associated with soil and litter, where they grow and feed,
- Group II – litter or epigeic animals, present mainly on the litter surface and able to move to other layers of ecosystem.

Table 3. Composition, annual mean density and % contribution in total density of soil-litter macrofauna communities in the forest and shelterbelts (S) of different age (years). Group I – soil fauna, Group II – epigeic fauna.

	Taxa	Forest		S (150)		S (6–7)		S (3–4)		S (1–2)	
		ind. m^{-2}	%	ind. m^{-2}	%	ind. m^{-2}	%	ind. m^{-2}	%	ind. m^{-2}	%
Group I	Insect larvae:										
	Diptera	150.0	15	173.3	7	288.4	21	167.5	14	552.5	45
	Coleoptera	215.0	21	793.3	33	301.3	22	267.5	23	117.5	9
	Heteroptera			36.7	2	15.0	1	7.5	<1	235.5	19
	Homoptera	10.0	1	36.7	2	13.1	1	27.5	2	12.5	1
	Others	5.0	<1	16.6	<1			57.5	5	10.0	1
	Lumbricidae	15.0	2	13.3	<1	5.0	<1	30.0	3		
	Enchytraeidae	20.0	2	6.7	<1	70.0	5	27.5	2		
	Symphyla	240.0	24	566.7	23	324.2	24	15.0	1	12.5	1
	Diplopoda			16.7	<1						
	Chilopoda	70.0	7	113.3	5	40.5	3	2.5	<1		
	Isopoda							5.0	<1	2.5	<1
	Total	725.0	72	1773.3	73	1057.5	79	607.5	52	942.5	76
Group II	Insect imagines:										
	Diptera	5.0	<1	23.3	1	21.9	2	47.5	4	152.5	12
	Coleoptera	25.0	3	90.0	4	58.7	4	47.5	4	27.5	2
	Staphylinidae	30.0	3	186.7	8	71.7	5	155.0	13	27.5	2
	Aphidoidea			16.7	<1	5.3	<1				
	Homoptera							12.5	1	2.5	<1
	Heteroptera			3.3	<1	0.9	<1			30.0	2
	Hymenoptera	10.0	1	86.7	4	32.2	2	30.0	3	22.5	2
	Formicidae	110.0	11	13.3	<1	32.2	2	160.0	14		
	Lepidoptera									2.5	<1
	Thysanoptera	50.0	5	93.3	4	53.6	4	22.5	2	17.5	1
	Araneae	50.0	5	110.0	5	12.8	1	82.5	7	17.5	1
	Pseudoscorpionidae			23.3	1						
	Total	280.0	28	646.7	27	289.4	21	557.5	48	300.0	24
	All macrofauna	1005.0		2420.0		1346.9		1165.0		1242.5	
	Number of taxa 25	15		21		17		19		17	
	H' index	3.12		3.10		3.06		3.42		2.56	

3. RESULTS

3.1. Composition and density of macrofauna

Twenty three taxa of studied animals were found in woodlots of different age, 10 of them were common for all sites (Table 3). The greatest taxonomic richness was found in the 150 years old shelterbelt (21 taxa) and the smallest – in the mixed forest (15 taxa). In view of the taxonomic richness of macrofauna, studied woods can be arranged in the following order according to their age: S (150) > S (3–4) > S (6–7) = S (1–2) > forest, while the H' index arranges the sites as follows: S (3–4) > forest > S (150) > S (6–7) > S (1–2).

Index of similarity of macrofaunal communities after Marczewski and Steinhaus (1959) shows that the 150 years old shelterbelt and the 6–7 years old one had most similar communities (0.81) while the most different appeared to be 6–7 and 1–2 years old shelterbelt (0.48) (Table 4, index 1). Forest macrofauna was the most similar in composition to that of the 6–7 years old adjacent shelterbelt and to the 3–4 years old one while it was more different from animal composition of the youngest shelterbelt. Along with the shelterbelt's age, its faunal composition becomes more similar to that in oldest shelterbelts.

Animal density in woods varied from 1005 ind. m^{-2} in the mixed forest to 2420 ind. m^{-2} in the 150 years old shelterbelt (Table 3, Fig. 1). There was a tendency of increasing animal density with age of the midfield shelterbelts. Differences in densities of the whole macrofauna and in particular groups and taxa between the woodlots were highly statistically significant (Table 5A).

Tabela 5. Statistical significance of the differences of mean values of animal densities (Groups: I – soil fauna, II – epigeic fauna and selected taxa) in the woods of different age (years) A. – for spatial and temporal series of data (analysis of variance, the Kruskall-Wallis test), B. – between pairs of sites (t-test), a-g animal communities as in Table 5A.

A.

	Taxa	spatial	temporal
a)	total macrofauna	**	n.s.
b)	Group I	**	*
c)	Group II	***	n.s.
d)	Dipteran larvae	*	*
e)	Coleopteran larvae	***	*
f)	Symphyla	***	***
g)	Chilopoda	***	n.s.

B.

	Forest	S (150)	S (6–7)	S (3–4)
S (150)	a ** f * b * c *			
S (6–7)		a ** e * c *** g *		
S (3–4)	f * g***	a ** e * b *** f *** g ***	b * f *** g **	
S (1–2)	f ** g ****	a ** e ** b * f ** c ** g **** d *	d e * g ****	d * e * g ****

$P < 0.05$** $P < 0.01$ *** $P < 0.001$ **** $P < 0.0001$

Table 4. Similarity index of animal communities in the forest and shelterbelts (S) of different age (in years): a – for all macrofauna, b – for dipteran larvae. 1 – similarity index of composition after Marczewski and Steinhaus (1959), 2 – similarity index of domination structure after Romaniszyn (1970).

		Forest		S (150)		S (6–7)		S (3–4)	
		1	2	1	2	1	2	1	2
S (150)	a	0.71	59.6						
	b	0.63	25.0						
S (6–7)	a	0.78	67.8	0.81	55.1				
	b	0.36	17.1	0.43	18.3				
S (3–4)	a	0.79	50.4	0.67	39.5	0.71	44.2		
	b	0.31	19.5	0.50	36.5	0.60	27.4		
S (1–2)	a	0.52	21.6	0.52	17.9	0.48	28.3	0.64	25.6
	b	0.29	8.9	0.46	12.1	0.67	15.7	0.64	27.4

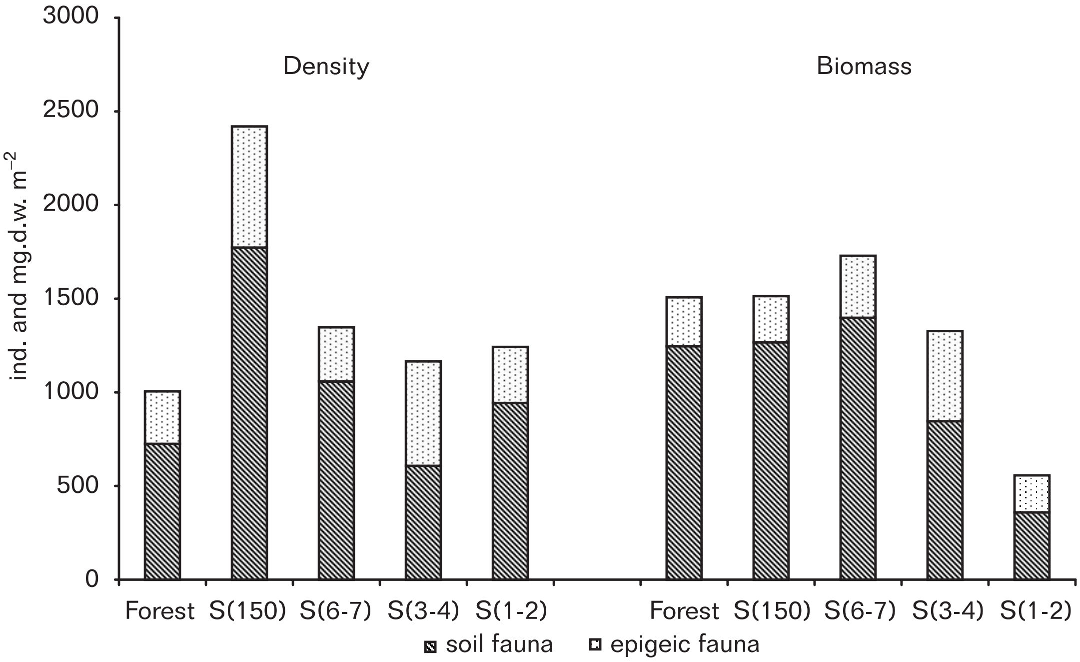

Fig. 1. Mean annual density and biomass of soil and epigeic macrofauna in woods: (mixed forest and midfield shelterbelts (S) of different age (in years).

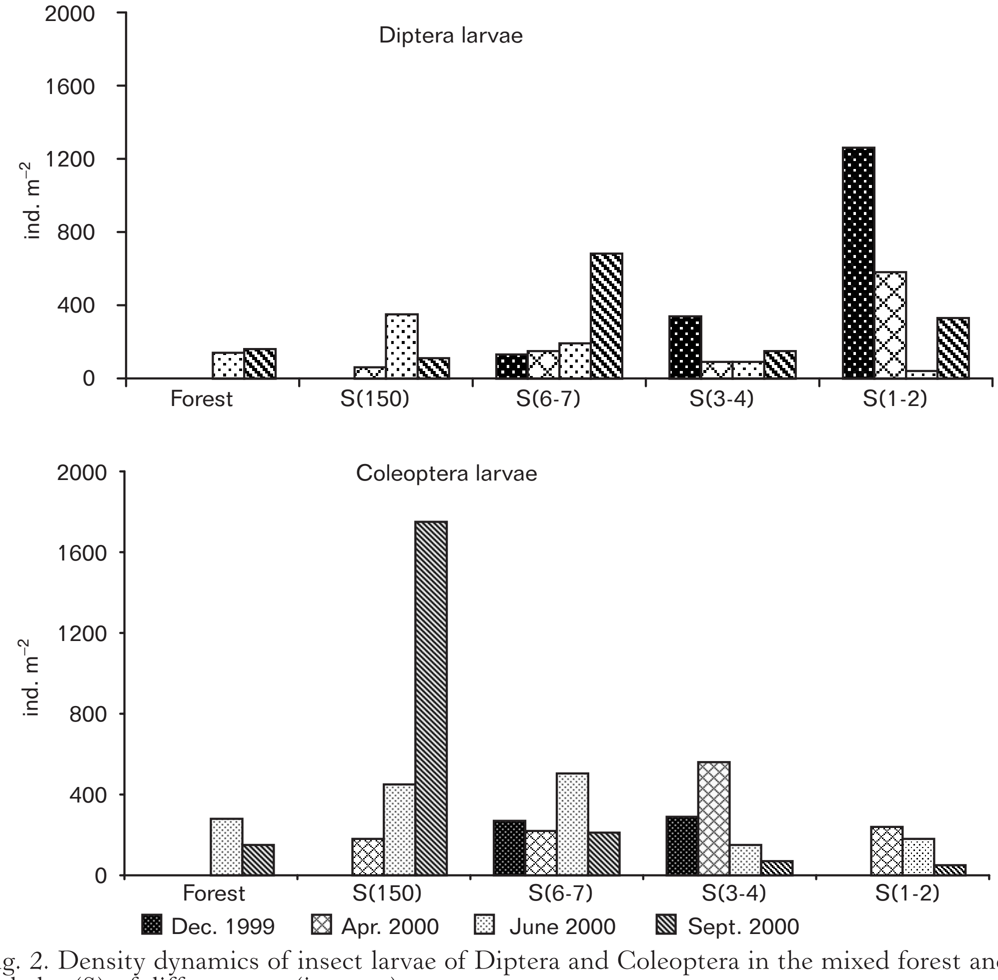

Fig. 2. Density dynamics of insect larvae of Diptera and Coleoptera in the mixed forest and shelterbelts (S) of different age (in years).

Statistical analysis of animal densities in pairs of sites showed the greatest differences between the oldest (S 150) and the youngest (S 1–2 and S 3–4) shelterbelts. There was no significant difference in animal density between the 6–7 years old shelterbelt and adjacent forest. The mixed forest and the 150 years old shelterbelt differed significantly in the densities of macrofauna from Group I and II and Symphyla. They also differed in the densities of Symphyla and Chilopoda from other shelterbelts. Thus, the trend of increasing differences in animal communities with increasing age of the woodlots was confirmed (compare the index of similarity in Table 4).

The most numerous taxa in the studied woods were dipteran larvae, coleopteran larvae and Symphyla (Table 3). Densities of the dipteran and coleopteran larvae varied considerably with time (Fig. 2) and the changes were statistically significant (Table 5A). Densities of coleopteran larvae differed significantly between the studied sites (Table 5B). The numbers of Symphyla and Chilopoda were closely associated with age of the shelterbelts (Table 3 and Fig. 3). Their presence and abundance may thus be an indicator of the growth (age) of the shelterbelt.

3.2. Composition and densities of dipteran larvae

Representatives of 16 families of dipteran larvae were recorded in the mixed forest and in the shelterbelts of different age. Four families: Asilidae, Cecidomyiidae, Dolichopodidae and Sciaridae were common for all sites (Table 6). The highest number of families was found in the 6–7 years old shelterbelt (13), the least – in the mixed forest (6). Younger shelterbelts showed also a great diversity of dipteran larvae (11–12 families). Most similar in composition were the communities of dipteran larvae in the 6–7 and 1–2 years old shelterbelts (0.67), the least similarity was found between the mixed forest and the youngest sshelterbelt (0.29) (Table 4, index 1). The older the shelterbelt the greater was its similarity in dipteran larvae composition to that in the mixed forest; *s* values ranged from 0.29 to 0.63 (Table 4, index 1).

Mean density of dipteran larvae varied from 150 in the mixed forest to 525.5 ind. m^{-2} in the youngest shelterbelt. In the forest, and in the 150 and 3–4 years old shelterbelts the densities of dipteran larvae were similar but definitely lower than in the youngest shelterbelt (Table 6, Fig. 4). The 1–2 years old shelterbelt

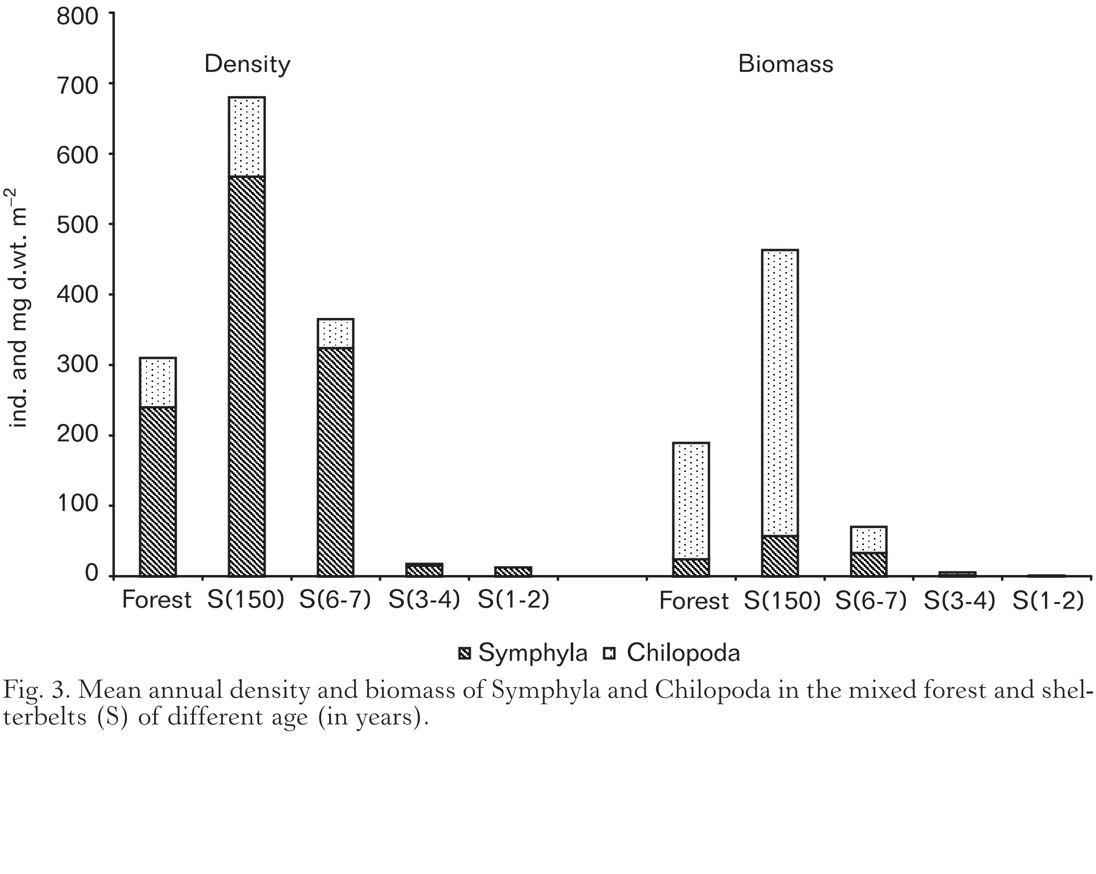

Fig. 3. Mean annual density and biomass of Symphyla and Chilopoda in the mixed forest and shelterbelts (S) of different age (in years).

differed significantly in the density of dipteran larvae from the 3–4 and from the 150 years old ones (Table 5B).

Larvae of Cecidomyiidae, Dolichopodidae and Sciaridae were most numerous and ubiquitous. Numerous, though not present in all sites were the larvae of Bibionidae, Rhagionidae and Chironomidae. Rhagionidae were found only in old woods while Bibionidae, Chironomidae, Stratiomyiidae, Theervidae and Tipulidae were typical for younger shelterbelts.

Woods of different age differed also in the composition of dominants and in the degree of domination (Table 6). Communities of dipteran larvae in the 150 and in the 3–4 years old shelterbelts were most similar in view of the domination structure (Table 4, index 2 =36,5), the least similar were those in the mixed forest and in the

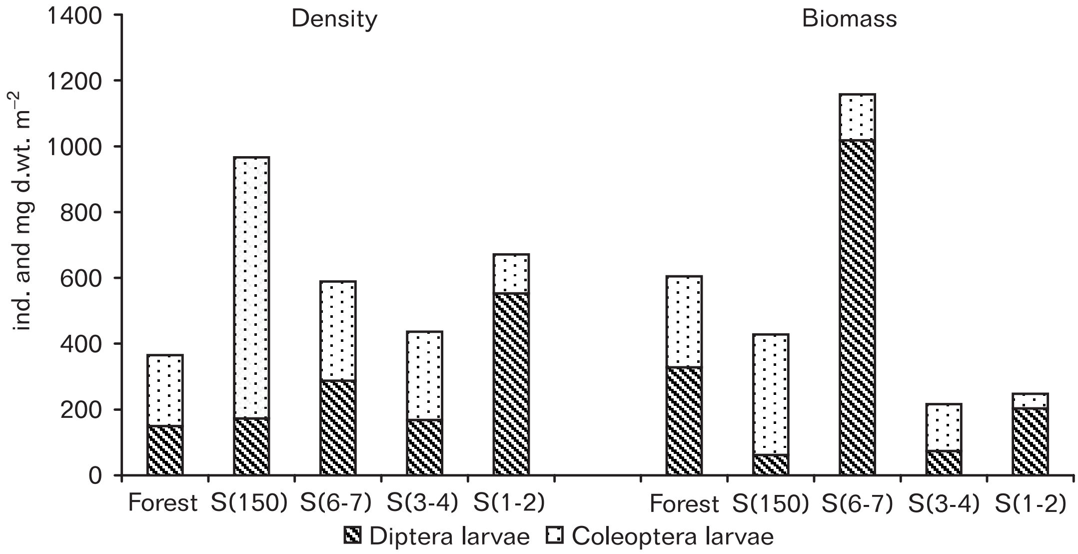

Fig. 4. Mean annual density and biomass of dipteran and coleopteran larvae in the mixed forest and shelterbelts (S) of different age (in years).

Table 6. Composition, annual mean density and domination structure of dipteran larvae communities in the forest and shelterbelts (S) of different age (years).

Families	Forest		S (150)		S (6–7)		S (3–4)		S (1–2)	
	ind. m^{-2}	%	ind. m^{-2}	%	ind. m^{-2}	%	ind. m^{-2}	%	ind. m^{-2}	%
Anthomyiidae					1.9	<1				
Asilidae	20.0	13	3.3	2	5.0	2	2.5	1	2.5	<1
Bibionidae					155.6	54	2.5	1		
Cecidomyiidae	35.0	23	66.7	39	53.8	19	90.0	54	60.0	11
Chironomidae					29.0	10	40.0	24	355.0	65
Dolichopodidae	15.0	10	13.3	8	18.6	6	7.5	5	10.0	2
Empididae			40.0	23	0.9	<1	2.5	1	2.5	<1
Muscidae									22.5	4
Psychodidae	5.0	3			1.0	<1				
Phoridae							2.5	1		
Rhagionidae	70.0	47	6.7	4						
Sciaridae	5.0	3	13.3	8	5.9	2	7.5	5	87.5	16
Sphaeroceridae			30.0	17	5.2	2	5.0	3	2.5	<1
Stratiomyiidae					7.0	2	5.0	3	2.5	<1
Therevidae					0.9	<1			2.5	<1
Tipulidae					3.6	1			2.5	<1
Trichoceridae							2.5	1	2.5	<1
Total	150.0		173.3		288.4		167.5		552.5	
Number of families	6		7		13		11		12	
H' index	2.05		2.32		2.18		2.13		1.72	

youngest shelterbelt (index 2 = 8.9). One may thus conclude that the domination structure of communities of dipteran larvae was differentiated.

Diversity of dipteran larvae measured with the H' index may be arranged in the following order according to the age of shelterbelts: S (150) > S (6–7) > S (3–4) > forest > S (1–2) (Table 6).

3.3. Biomass of macrofauna

In spite of considerable differences in densities between the mixed forest and the 150 years old shelterbelt, biomass of macrofauna was similar in the two sites (Fig. 1). In younger shelterbelts (1–7 years old) the biomass of the total macrofauna and that of Group I tended to increase with age. The contribution of animals of Group I to the total biomass was higher than those of Group II and varied between 64% in the youngest shelterbelt and 84% in the oldest one (Table 7). Domination of particular taxa changed, in similar way as the densities. Lumbricidae occurred scarcely but they dominated in biomass in the mixed forest, in 3–4 and in the 150 years old shelterbelts. Similarly, Chilopoda had the highest contribution to the total biomass in the 150 years old shelterbelt and were one of the biomass dominants in the mixed forest. Symphyla, however, with their high densities had a small share in biomass (Table 7, Fig. 3).

Most numerous taxa like dipteran and coleopteran larvae produced also high biomass, particularly the former; their contribution to the total biomass in the 6–7 years old shelterbelt amounted 59% (Table 7). Percentage biomass of coleopteran larvae varied from 8% in the 6–7 to 24% in the 150 years old shelterbelts and there was a tendency of increasing biomass with the wood's age (Fig. 4).

Biomass of dipteran larvae varied from 74.4 mg d.wt. m^{-2} in the 150 years old to 1017.5 mg d.wt. m^{-2} in the 6–7 years old shelterbelt (Fig. 4). Larvae of Bibionidae, Rhagionidae, Chironomidae, Dolichopodidae and Stratiomyiidae contributed most to biomass in all woods (Table 8). Each site had different composition of dominants. Biomass in the mixed forest was dominated

Table 7. Percentage contribution to the total biomass of soil-litter macrofauna in the forest and shelterbelts (S) of different age (years). Group I – soil fauna, Group II – epigeic fauna.

	Taxa	Forest	S (150)	S (6–7)	S (3–4)	S (1–2)
Group I	Insect larvae:					
	Diptera	22	4	59	6	37
	Coleoptera	18	24	8	11	8
	Heteroptera		<1	<1	<1	7
	Homoptera	<1	<1	<1	<1	<1
	others	1	1		2	11
	Lumbricidae	28	13	8	42	
	Enchytraeidae	<1	<1	2	2	
	Symphyla	2	4	2	<1	<1
	Diplopoda		10			
	Isopoda				1	<1
	Chilopoda	11	27	2	<1	
	Total	83	84	81	64	64
Group II	Insect imagines:					
	Diptera	<1	<1	<1	<1	5
	Coleoptera	5	6	14	15	19
	Staphylinidae	1	4	2	4	2
	Aphidoidea		<1	<1		
	Heteroptera		<1	<1		7
	Homoptera				<1	<1
	Hymenoptera	<1	1	<1	<1	<1
	Formicidae	7	1	2	11	
	Lepidoptera					<1
	Thysanoptera	<1	<1	<1	<1	<1
	Araneae		3	2	<1	4 1
	Pseudoscorpionidae		<1			
	Total	17	16	19	36	36

by Rhagionidae larvae, in the 150 years old shelterbelt – larvae of Dolichopodidae were dominating with a considerable share of Rhagionidae and Empididae (all are predatory larvae). The 6–7 years old shelterbelt was dominated by saprophagous Bibionidae (89%), 3–4 years old – by zoophagous Stratiomyiidae and Dolichopodidae and by saprophagous Chironomidae and 53% of biomass in the youngest shelterbelt (1–2 years old) consisted of Chironomidae.

Table 8. Percentage contribution of dipteran larvae to their total biomass in the forest and shelterbelts (S) of different age (years).

Families	Forest	S (150)	S (6–7)	S (3–4)	S (1–2)
Anthomyiidae			<1		
Asilidae	15	3	<1	<1	10
Bibionidae			89	2	
Cecidomyiidae	1	12	<1	12	3
Chironomidae			<1	17	54
Dolichopodidae	17	35	<1	21	2
Empididae		19	<1	<1	<1
Muscidae					3
Psychodidae	<1		<1		
Phoridae				7	
Rhagionidae	66	19			
Sciaridae	1	7	<1	4	11
Sphaeroceridae		5	<1	2	1
Stratiomyiidae			4	34	12
Therevidae			<1		<1
Tipulidae			4		2
Trichoceridae				<1	<1

3.4. Trophic structure of macrofauna

A tendency was observed of increasing densities of saprophages and herbivores from the mixed forest to the youngest shelterbelt and, at the same time, of decreasing share of predators. The only exception from this rule was 3–4 years old shelterbelt, where saprophages were the least numerous and where zoophages dominated (Fig. 5).

Biomass values displayed a different trend. In old woodlots (mixed forest and S 150) the trophic structure of biomass was almost identical, i.e. the greatest share of zoophages, high contribution of saprophages and small contribution of phytophages. Saprophages achieved the greatest share in biomass in the 6–7 years old shelterbelt but it decreased in the youngest shelterbelt (Fig. 5).

Trophic structure of dipteran and coleopteran larvae showed the interesting changes in woods of different age (Fig. 6). There was less saprophagous dipteran larvae and more zoophagous larvae in old woods than in the younger ones. Biomass of these trophic groups followed the same pattern with the exclusion of 6–7 years old shelterbelt, where proportions between the trophic groups were interfered by mass appearance of saprophagous Bibionidae larvae.

Different relations were observed in coleopteran larvae. Contribution of phytophages increased with age of the woods and

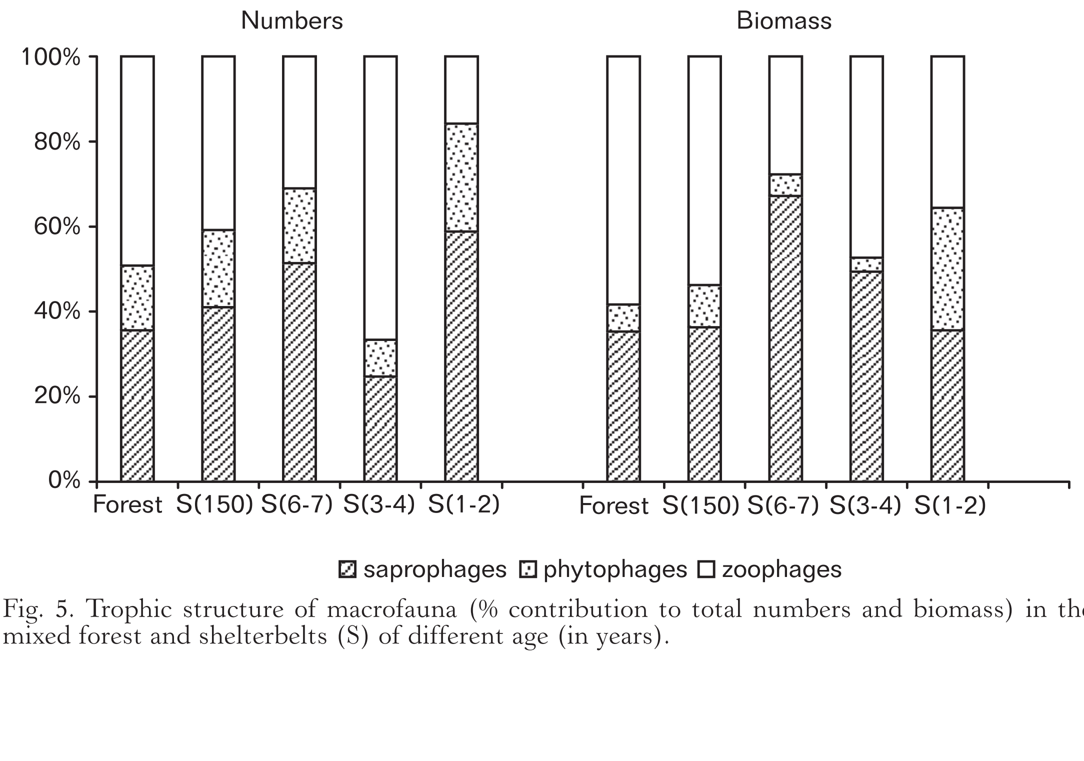

Fig. 5. Trophic structure of macrofauna (% contribution to total numbers and biomass) in the mixed forest and shelterbelts (S) of different age (in years).

zoophages showed a similar contribution in all sites except the 3–4 years old shelterbelt, where the contribution of predators was very high. The youngest shelterbelt was characterised by the highest share of saprophages and the lowest share of phytophages both in biomass and densities.

3.5. Mean individual weight in animal communities

The smallest mean biomass of an individual of all macrofauna was found in the youngest shelterbelt (0.45 mg.d.wt.) and the biggest one in mixed forest (1.50 mg.d.wt.). In the 6–7 and 3–4 years old shelterbelts, the average biomass of an individual was quite high (Table 9).

The youngest shelterbelt was characterised by the smallest animals of all groups. Small individuals were also found

Table 9. Average individual weight (mg d.wt.) of animal groups in the forest and shelterbelts (S) of different age (years).

Communities	Forest	S (150)	S (6–7)	S (3–4)	S (1–2)
Total macrofauna	1.50	0.61	1.28	1.14	0.45
Diptera larvae	2.18	0.36	3.53	0.44	0.37
Coleoptera larvae	1.29	0.46	0.47	0.53	0.38
Saprophages	1.49	0.52	1.68	0.28	0.27
Phytophages	0.63	0.34	0.37	0.43	0.51
Zoophages	1.77	1.95	1.15	0.81	1.01

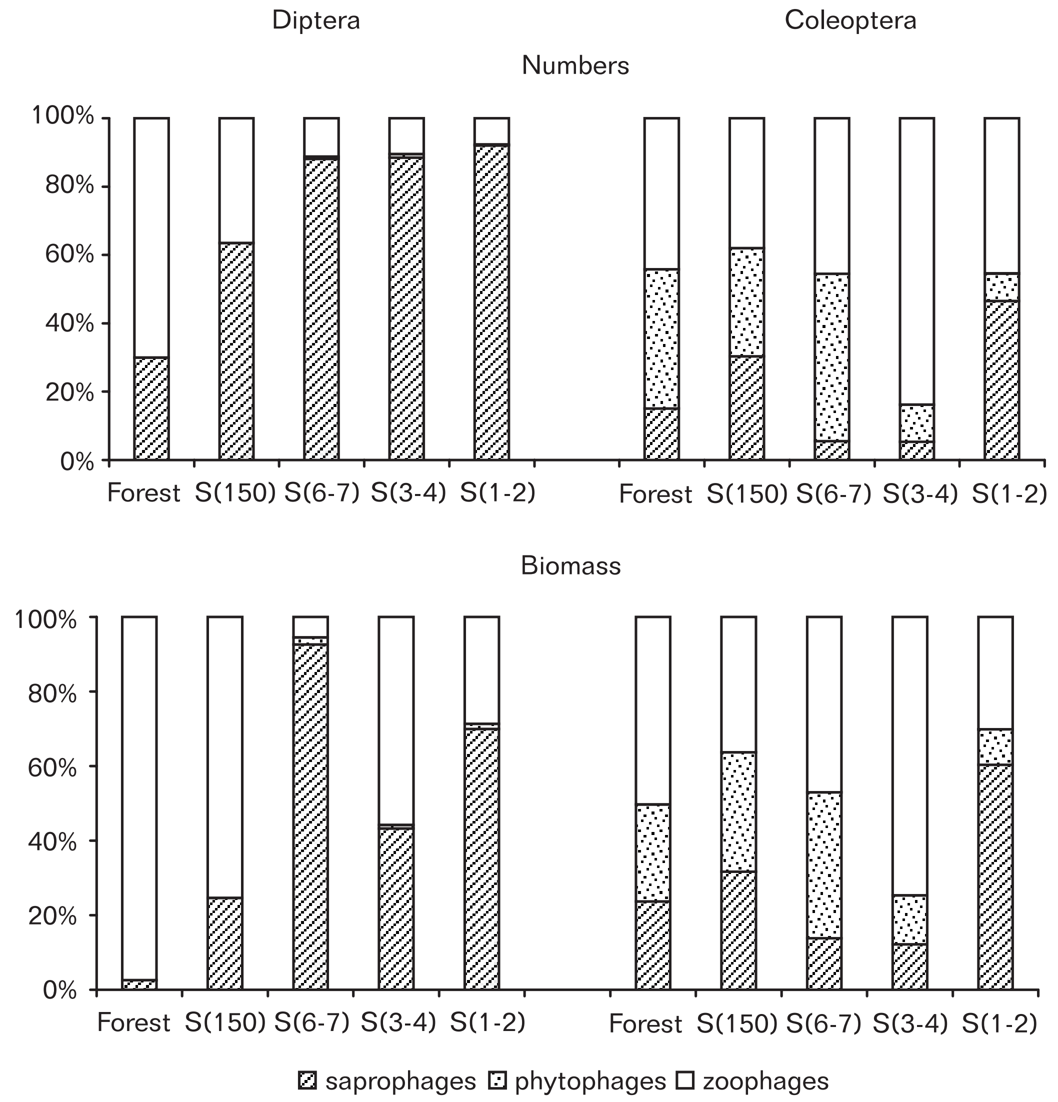

Fig. 6. Trophic structure of dipteran and coleopteran larvae in the mixed forest and shelterbelts of different age (in years).

in the oldest one (150 years old), apart from zoophages; their mean biomass was relatively high. The mixed forest and the 6–7 years old shelterbelt was characterised by high biomass of an average individual.

3.6. Succession of soil-litter animals in the midfield shelterbelts

Comparing the shelterbelts of different age allowed to establish a sequence of colonisation of a new shelterbelt by soil-litter animals and to follow the subsequent stages of succession. Comparison of three younger shelterbelt (1–7 years old) on the first date of sampling (October 1999) showed that the density of dipteran larvae in the 1 year old strip was about 4 times higher than in the 3 years old strip and 11 times higher than in the 6 years old strip (Fig. 2, Table 10). The densities clearly decreased with age of the shelterbelt.

Newly established shelterbelt was mainly colonised by dipteran larvae, which composed 92% of abundance of all macrofauna (Table 10). Within dipteran larvae the dominating families were Chironomidae (70%) and Sciaridae (21%). Coleoptera were not present in the 1 year old shelterbelt, neither larvae nor imagines. Pioneers in colonization were thus dipteran larvae and in smaller degree (5%) – larvae of Heteroptera. New woodlot was characterised by the highest density and the lowest diversity of inhabiting animals as compared with older shelterbelts.

Larvae and adults of beetles and of Symphyla appeared in the second year of the woodlot growth apart from the still numerous dipteran larvae. Densities of these animals increased with the shelterbelt age. In the second year, heteropteran larvae achieved maximum densities, which then decreased in older shelterbelts. Chilopoda appeared in small numbers in 4 years old shelterbelt and showed maximum densities in old shelterbelt (S 150) (Table 10, Fig. 3).

As already mentioned, within dipteran larvae, Chironomidae and Sciaridae were those, which developed in great numbers in newly established shelterbelts. The numbers decreased markedly with age of shelterbelt (Table 10). Larvae of Cecidomyiidae and Dolichopodidae appeared in the spring next year and their numbers increased with age of the shelterbelts. Larvae of Rhagionidae appeared only in old woods.

The highest animal density (mainly dipteran larvae), the least diversity and the lowest animal biomass were found in new planted shelterbelts. Biodiversity of animals and mean individual weight of a representative of macrofauna increased with the shelterbelt age.

Table 10. Succesion (density and biomass) of more common taxa of soil macrofauna in shelterbelts of different age.

Sampling period	Sept. 1999			Apr. 2000				Mean annual in 2000				
Age of shelterbelts (years)	1	3	6	1.5	3.5	6.5	150	2	4	7	150	120 Forest
Number of taxa	5	9	12	12	15	12	14	16	18	17	21	15
						ind. m^{-2}						
Total macrofauna	1670	1100	600	2200	1540	1710	710	1100	1187	1596	2420	1005
Diptera larvae (all)	1540	400	140	890	140	180	80	427	153	367	197	150
Chironomidae	1080	160	40	800	20	40	0	273	38	27	0	0
Sciaridae	330	40	0	20	20	0	20	20	10	15	20	5
Cecidomyiidae	0	180	10	0	80	100	50	80	93	80	77	35
Dolichopodidae	0	10	50	0	10	20	0	13	8	8	13	15
Rhagionidae	0	0	0	0	0	0	10	0	0	0	7	70
Coleoptera larvae	0	290	270	240	560	220	180	157	260	312	793	215
Coleoptera imagines	0	310	50	110	100	10	100	74	166	157	277	55
Staphylinidae	0	280	40	40	80	0	60	37	113	82	187	30
Symphyla	0	0	20	40	60	950	20	17	20	426	567	240
Chilopoda	0	0	20	0	10	60	200	0	3	47	113	70
						mg d. wt. m^{-2}						
Total macrofauna	638	745	897	793	2401	620	1972	530	1494	2006	1514	1506

4. DISCUSSION

Newly established shelterbelts on croplands, which might be compared with fresh barren lands are immediately colonised by animals, mainly by mobile adult insects (Karg 1995). The animals find favorable conditions there to hide, to lay eggs and to grow next generations due mainly to the cessation of agrotechnical management and to the abundant growth of vegetation (Bernacki 2004). Intensity and character of colonisation depends on many factors e.g. on the soil origin (Szujecki 1990) and on the last crop (Frouz 2001). Equally important are climatic conditions, terms of shelterbelt planting (autumn *versus* spring) and a variety of habitat factors. All this makes a great variability of the numbers and composition of animal communities (1–19 taxa of epigeic insects – Karg 2004) colonising young (0–1 years old) shelterbelts. One may thus expect that secondary succession may proceed in a different way and with different intensity in different shelterbelts. In the 1–2 years old shelterbelt the lowest number of epigeic taxa was found by Karg (2004), and the taxonomic richness of soil animals (5 taxa) was also low. The diversity rapidly increased in the next year to achieve the taxonomic richness (12–15 taxa) typical for older shelterbelts. Decisive dominants at that time were dipteran larvae (over 90% of all macrofauna) and most numerous within this group were the larvae of Chironomidae and Sciaridae (over 90% of dipteran larvae). The density of Chironomidae in this shelterbelt was 7 times higher than in the 3 years old shelterbelt and 27 times higher than in the 6 years old one. The numbers of Sciaridae were 8 and 330 times higher, respectively. So, dipteran larvae initiate the succession on newly established shelterbelts and larvae of Chironomidae and Sciaridae families are the pioneers in colonisation. Larvae of Cecidomyiidae appear in the next stage accompanying the still present dipteran larvae. Density of Cecidomyiidae increases with the shelterbelts ageing to achieve maximum in the 3–4 years old shelterbelts. So, the diversity of dipteran larvae increases but at the same time their numbers decline. Such successional trend on young barrow lands or shelterbelt was confirmed in other studies like Hutson 1980, Struve-Kusenberg 1981, Frouz 1994 and Borowski 1995. Dipteran larvae are one of the most numerous taxa in the soil macrofauna not only in shelterbelts but also in other ecosystems and their density varies usually in a broad range (Paplińska 1980, 1984, Olechowicz 1986, 1998, Frouz 2001).

In the second year of existence the shelterbelt is colonised by coleopteran larvae and imagines, which appear in numbers similar to those in older shelterbelts. The numbers of Coleoptera increase with the shelterbelts age as does the density, biomass and diversity of all macrofauna. Similar tendency was observed in butterfly communities from mid-field shelterbelts of different age (Sobczyk 2004), in herb-layer entomofauna of old and young shelterbelts (Ryszkowski *et al.* 1999) and in larvae of soil insects developing in forest plantings on post-crop lands (Szujecki 1990). The tendency is reasonable since during the shelterbelt growth trees produce more litter (its biomass increases to the 6th year after planting, Bernacki 2004). Diversity and biomass of the forest undergrowth also increases up to the 5th year (*ibidem*). Development of the shelterbelt is followed by changes in soil, e.g. by the increased soil organic matter content (Kostro-Chomać 2003, Wojewoda and Russel 2003). Therefore, the biomass of soil macrofauna attains its maximum in the 6–7 years old shelterbelt.

The stages of secondary succession of animal communities in midfield shelterbelts involved 7 years. Final stages were estimated upon the analysis of quite different old woods: a mixed forest and the 150 years old shelterbelt. This last one differed from other shelterbelt in age but also in the tree stand composition formed by mainly one tree species – *Robinia pseudoacacia*. This strip had a typically thick litter layer of a high organic carbon and nitrogen content and low pH; its soil had pH lower than in younger shelterbelts (Table 1, also in Kostro-Chomać 2003). Moreover, the undergrowth vegetation is rather scanty there. All these factors may interfere with the regularities described above. Although animal diversity and densities were highest in the 150 years old shelterbelt, biomass of soil animals was lower than in the younger shelterbelts. Average individual biomass of particular animal groups and taxa were relatively small there, especially in dipteran larvae and in phytophages. Only zoopha-

ges were the largest in this shelterbelt. A tendency of increasing individual biomass of soil animals with the shelterbelt age was found in younger (1–7 years old) shelterbelts. This was also true for the forest, where an average individual had the largest biomass. The advancement of succession is associated with higher individual biomass (Szujecki 1990). "Diminution" of individuals in the oldest shelterbelt is an evidence of a different course of succession in this site and in the mixed forest and suggests impoverishment and transformation of the former habitat. Possibly allelopathic substances excreted by acacia are responsible for this difference. It seems that the oldest shelterbelt, similarly to the youngest, looses more energy on animal metabolism (Reichle 1971) than other shelterbelts and particularly the mixed forest.

Smaller density, biomass and diversity of soil-litter animals found in the mixed forest, as compared with midfield shelterbelts probably reflect the real difference between the functioning of both ecosystems. Some references show that young shelterbelts in the successional phase or those functioning as small habitat islands are characterised by higher values of these parameters than an old forest on large area (Dąbrowska-Prot 1999, Szujecki 1990).

Similarity in the soil animal communities between the wood strip and the forest increases with age of the former. The distance between a wood strip and a forest is also important and therefore the 6–7 years old shelterbelt situated near the forest did not significantly differ in densities of particular animal taxa, contrary to other shelterbelts situated farther. The two habitats had the highest indices of similarity of soil invertebrates. This is an evidence of the important effect of forest on animal communities in newly established midfield shelterbelts and may suggest that the 6–7 years old shelterbelt is a fully "matured" ecosystem similar to the 120 years old mixed forest.

5. CONCLUSIONS

1. Dipteran larvae, which comprised 90% of density of all soil and litter animals were the pioneers in colonising newly established shelterbelts (Table 10). Two families: Chironomidae and Sciaridae dominated among dipteran larvae, their combined contribution to the total density amounted 92%. Densities of these larvae markedly decreased with the shelterbelt age. Densities and percentage contribution of Dolichopodidae and Cecidomyiidae increased with shelterbelt age. The same effect was observed for Rhagionidae, which were found exclusively in the old woodlots (150 years old shelterbelt and 120 years old mixed forest). In subsequent years of the mid-field woodlot succession marked changes in dipteran larvae community were noted. Biodiversity measured with the H' index increased as did taxonomic richness, which increased during the initial 7 years to decrease again in older woodlots (Table 6). Trophic structure of dipteran larvae also changed with time, which manifested itself in decreasing numbers of saprophagous larvae and increasing contribution of predators (Fig. 6).

   The second numerous taxon of macrofauna – Coleoptera – colonised woodlots in the second year. Density of these animals increased with the shelterbelt age (Tables 3, 10, Fig. 3). Similar tendency was recorded for Symphyla. Chilopoda did not appear in shelterbelts younger than 4 years and their densities increased with age.
2. The following trends were observed along with the shelterbelt ageing:

– increasing numbers of all macrofauna and particularly of some taxa (Symphyla, Chilopoda, coleopteran larvae and imagines and some dipteran larvae like Dolichopodidae, Cecidomyiidae and Rhagionidae (Tables 3, 6),
– increasing biomass of all macrofauna, of animals from the Group I (soil fauna) and of coleopteran larvae (Figs 1, 4),
– increasing share of zoophages in all macrofauna (Fig. 5) and in dipteran larvae (Fig. 6),
– increasing share of phytophages in coleopteran larvae communities (Fig. 6),
– increasing average individual biomass (Table 9),
– increasing taxonomic richness and the H' index (Tables 3, 6),
– increasing similarity of composition and domination structure of all macrofauna and of dipteran larvae to those in forest communities (Table 4),
– decreasing density of dipteran larvae,

particularly of Chironomidae and Sciaridae (Table 6),
– decreasing share of saprophages in all macrofauna (Fig. 5) and in dipteran larvae (Fig. 6).

3. Composition and density of animals in new shelterbelts, where small tree seedlings occur, suggest that wide balks left unploughed can play the similar role in the enriching soil fauna of croplands.
4. The greatest similarity of densities, composition and domination structure of animals between the 6–7 years old shelterbelt and adjacent mixed forest is an evidence that the shelterbelts are in fact ecological corridors penetrated by fauna from the neighbouring forest complexes.

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