Baltic J. Coleopterol. 11(2) 2011
ISSN 1407 - 8619

Abundance and composition of Geotrupidae (Coleoptera: Scarabaeoidea) in the developmental cycle of pine stands in Człuchów Forest (NW Poland)

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Byk A. 2011. Abundance and composition of Geotrupidae (Coleoptera: Scarabaeoidea) in the developmental cycle of pine stands in Człuchów Forest (NW Poland). *Baltic J. Coleopterol., 11(2): 171 - 186.*

The study aimed at discovering the changes in abundance and composition of Geotrupidae communities in the developmental cycle of pine stands. Beetles were collected with the aid of bait traps in Człuchów Forest (Polish: Lasy Człuchowskie) in the years 1998-1999. In total, 69389 specimens were collected, representing 5 species. The obtained results showed that the structure of Geotrupidae communities in pine stands changed in the course of forest developmental cycle. Brownfields adjoining to forests, clear-cut areas and forest plantations were inhabited by heliophilous communities of Geotrupidae typical of pine forests, with *Trypocopris vernalis* (Linnaeus, 1758) as a superdominant. Thicket, pole timber and mature stands were inhabited by umbrophilous Geotrupidae typical of forests, with *Anoplotrupes stercorosus* (Scriba, 1791) as a superdominant. The abundance of Geotrupidae communities grew as the pine stands matured, increasing from the stage of forest plantations until the pole timber stage, and then decreasing again in mature stands.

Key words: Geotrupidae, *Anoplotrupes, Trypocopris, Geotrupes, Typhaeus,* coprophagous beetles, forest areas, pine stands, Poland.

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INTRODUCTION

Representatives of the family Geotrupidae Latreille, 1802 are common in the Holarctic region. As for Geotrupidae encountered in Palearctics, there can be found the representatives of two subfamilies: Lethrinae Mulsant & Rey, 1871 and Geotrupinae Latreille, 1802. The subfamily Lethrinae is represented in Palearctics by a single genus, *Lethrus* Scopoli, 1777, comprising 112 species, out of which 8 are ecnountered solely in Europe. The subfamily Geotrupinae is represented in Palearctics by 11 genera and 184 species, out of which 53 are found solely in Europe (Löbl & Smetana 2006). Even though the Geotrupidae are a comparatively well-studied group with regard to taxonomy, new species are still identified within this group, not only in the poorly investigated regions of East Asia, but also in Europe. In Central Europe 8 species have been identified so far: *Anoplotrupes stercorosus* (Scriba, 1791), *Geotrupes mutator* (Marsham, 1802), *G. spiniger* (Marsham, 1802), *G. stercorarius* (Linnaeus, 1758), *Trypocopris* *alpinus* (Sturm & Hagenbach, 1825), *T. vernalis* (Linnaeus, 1758), *Typhaeus typhoeus* (Linnaeus, 1758) and *Lethrus apterus* (Laxmann, 1770). The presence in Poland of two of these, namely *T. alpinus* and *L. apterus,* is highly problematic.

The Geotrupidae include saprophagous species, among which coprophagy dominates as a type of dietary specialization. Young stages feed on faeces, while adult forms feed mainly on the suspension contained in the liquid fraction of faeces (Rojewski 1980). Crovetti et al. (1984) and Martín-Piera & López Colón (2000) point out the necrophagous tendencies of the imago forms of coprophagous Geotrupidae species found in Spain. Individuals of *T. typhoeus* are sometimes found directly underneath the carcasses of dead animals (author's observation). The larvae of *A. stercorosus* feed on litter in the form of provision mass brought underground by imagines. Imagines of this species feed on mouldy litter, animal faeces, sporocarps of umbrella mushrooms and the juice of trees (Rojewski 1980, Burakowski et al. 1983). The genus *Lethrus* is represented by sapro-phytophagous species. Imagines place cut grass leaves in their underground nests, on which the larvae feed once the leaves have fermented.

The coprophagous Geotrupidae are either paracopric or telecopric; their imagines dig tunnels, either under the faeces or in their proximity. These tunnels end in brood chambers, where the imagines place faeces on which their larvae can feed. The depth and diameter of the tunnels, as well as the shape, number and distribution of brood chambers are characteristic features of a species and allow for its identification. A majority of species representing the family in question dig tunnels up to 40 cm deep. The depth of tunnels dug by *T. typhoeus*, encountered in Europe, sometimes reaches up to 140 cm (Brussard & Visser 1987).

In subject literature published in various countries there can be found a number of studies focusing on the complexity of the relationship between a coprophage and its environment (Rainio 1966, Desiere 1973, Koskela & Hanski 1977, Grosfilley & Buisson 1982, Henry & Prelle 1986, Hanski & Cambefort 1991, Lobo 1993, Wassmer 1995, Mittal & Bhati 1998).

Information about species representing the family Geotrupidae in Poland can be found either in more extensive studies focusing on the superfamily Scarabaeoidea (Hildt 1896, Breymeyer 1974, Stebnicka 1976 a,b, Burakowski et al. 1983, Bunalski 1999, Górz 2007) or scattered across a variety of sources. A considerable number of studies tackles the problematics of biology and ecology of *A. stercorosus.* Borowski (1960) highlighted the role played by this beetle species in enhancing aeration, permeability and fertilization of forest soil. Olszewski (1979) pointed out a significant interdependency between the number of collected individuals of *A. stercorosus* and the air temperature at the forest bottom. Rembiałkowska (1982) described the dynamics of development of this species. Plewińska (2007) proved that rodent faeces were more attractive for *A. stercorosus* in comparison with cow or horse faeces and had a large share in its diet. Byk & Semkiw (2010) specified habitat preferences of *A. stercorosus.* The studies by Breymeyer (1978), Rembiałkowska (1980) and Rojewski (1980) touched upon the subject of the significance of coprophagous beetles in meadow and forest ecosystems.

In the recent years it has been brought to attention that the Geotrupidae can be utilized as zooindicators of environmental condition (Szwałko 1995, Szwałko & Starzyk 1997, Skłodowski et al. 1998, Klimaszewski & Strużyński 2005, Skłodowski & Duda 2007). However, in spite of the enormous role played by the Geotrupidae in forest environment and their usefulness in monitoring changes taking places in ecosystems, the acquaintance with their ecoogical requirements is still unsatisfactory. The necessity to obtain a more complete picture of Geotrupidae communities found in pine forests of lowland areas in the Pomeranian Lake District (Polish: Pojezierze Pomorskie) was the reason to undertake studies on the following:

- abundance and composition of Geotrupidae communities in pine stands;
- identification of dominant species and Geotrupidae communities characteristic of particular phases of the developmental cycle of pine stands;
- investigation of the character of changes taking place in species composition and abundance of Geotrupidae communities in connection with tree stand development.

Taking into account the fact that the family Geotrupidae is represented in Poland by merely 6 coprophagous species, among which the most common forest species is *A. stercorosus*, feeding on forest litter, and the fact that as the forest matures the humus layer is becoming thicker, the study has been based on the hypothesis that the abundance of Geotrupidae communities grows as the pine stands mature, while the number of species becomes reduced.

MATERIAL AND METHODS

Człuchów Forest (Polish: Lasy Człuchowskie) is situated within the geobotanical region of Pomeranian Divide, the syntaxonomical region of Sandar Forefields of Central Pomeranian Lake District (Polish: Kraina Sandrowych Przedpoli Pojezierzy Środkowopomorskich) and the syntaxonomical subregion of Wałcz (Polish: Podkraina Wałecka) (Fig. 1).

Fig. 1. Location of Człuchów Forest within the territory of Poland

The region is characterized by a considerable areage of sandur lowlands, with the landscape of coniferous forests and mixed forests with the association of *Leucobryo-Pinetum* characteristic of coniferous forests and the associations of *Fago-Quercetum* and *Querco-Pinetum* characteristic of mixed forests (Matuszkiewicz 1993). Study sites were located in tree stands belonging to Niedźwiady Forest Inspectorate and the adjacent tree stands belonging to Osusznica Forest Inspectorate. The area was covered by a compact forest complex, mostly by coniferous forest (ca. 90%), of which ca. 80% was fresh coniferous forest. The coniferous forest comprised mainly pines with a small admixture of spruces and birches (Plan Urządzania Lasu 1992).

For purposes of the study 20 study sites were established, selected in such a way so as to represent a sequence of the successive stages of forest developmental cycle , i.e. land before afforestation (brownfield adjoining to a forest, clear-cut), forest plantation, thicket, pole timber and mature stand (Tab. 1).

In each study site, 5 ground traps baited with portions of cow manure (10 cm^3) were set (Fig. 2). The size of a single portion of cow manure was specified on the basis of the assumption that the amount of bait should allow to acquire knowledge about the complete species composition of a particular beetle community, but should neither alter the nutritional conditions within a given area nor attract individuals from beyond this area. During the study 100 traps were set in each site, arranged in a square with twenty-meter sides, and with marked diagonals (so-called "envelope"). Insects were collected at monthly intervals from April till October, in 1998 and 1999.

The systematic hierarchy and names of particular species were quoted after the "Catalogue of Palearctic Coleoptera" (Löbl & Smetana 2006). While specifying the pattern of domination, the scale applied by Kasprzak & Niedbała (1981) was utilized: superdominants – > 30.00%, dominants – 5.01 – 30.00%, subdominants – 1.01 – 5.00% and accidental species – d< 1.00%.

Symbol of study site	Forest district	Forest compartment	Stage of forest developmental cycle	Stand age	Plant community type
LBA1	Stara Brda	–	land before afforestation (fallow land)	–	*Sedo-Scleranthetea*
LBA2	Stara Brda	–	land before afforestation (fallow land)	–	*Molinio-Arrhenatheretea*
LBA3	Brzeźno	249d	land before afforestation (clear-cut area)	–	*Epilobio-Senecionetum silvatici*
LBA4	Pustowo	169h	land before afforestation (clear-cut area)	–	*Epilobio-Senecionetum silvatici*
FP1	Pustowo	118b	forest plantation	2	*Epilobio-Senecionetum silvatici*
FP2	Stara Brda	92j	forest plantation	2	*Epilobio-Senecionetum silvatici*
FP3	Stary Most	293a	forest plantation	4	*Sedo-Scleranthetea*
FP4	Stara Brda	88a	forest plantation	2	*Sedo-Scleranthetea / Vaccinio-Piceetea*
T1	Pustowo	139f	thicket stage	12	*Sedo-Scleranthetea / Vaccinio-Piceetea*
T2	Stara Brda	60f	thicket stage	11	*Leucobryo-Pinetum*
T3	Stara Brda	66j	thicket stage	12	*Sedo-Scleranthetea / Vaccinio-Piceetea*
T4	Stara Brda	63k	thicket stage	11	*Epilobio-Senecionetum silvatici*
P1	Stara Brda	65k	pole timber stage	50	*Sedo-Scleranthetea / Vaccinio-Piceetea*
P2	Stara Brda	83a	pole timber stage	42	*Leucobryo-Pinetum*
P3	Stara Brda	88c	pole timber stage	50	*Sedo-Scleranthetea / Vaccinio-Piceetea*
P4	Stary Most	293i	pole timber stage	48	*Leucobryo-Pinetum*
MS1	Stara Brda	63b	mature stand	90	*Leucobryo-Pinetum*
MS2	Stara Brda	61b	mature stand	105	*Leucobryo-Pinetum*
MS3	Stara Brda	91a	mature stand	110	*Leucobryo-Pinetum*
MS4	Pustowo	168a	mature stand	90	*Leucobryo-Pinetum*

The evaluation of preferences of particular species representing the family Geotrupidae with respect to specific phases of the developmental cycle of pine stands was conducted by implementing the PCA method, using the program CANOCO 4.0 (Ter Braak & Smilauer 1997). The PCA analysis of Geotrupidae communities was

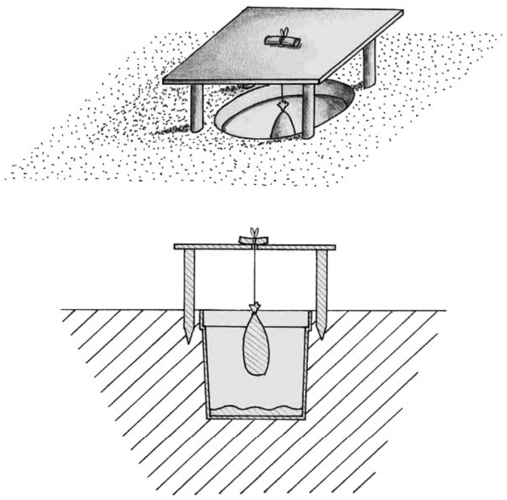

Fig. 2. A baited ground trap for collecting Geotrupidae in pine stands in Człuchów Forest, 1998-1999 (drawing by J. Piętka)

performed after having previously checked the gradient length by the DCA method; since it was lower than 3 units, the performance of a linear analysis was advisable. The faunistic similarity of Geotrupidae communities inhabiting various phases of the developmental cycle of pine stands was calculated by means of cluster analysis, utlizing Ward's method, and Euclidean distance was utilized as the measure of similarity. The statistical analysis was performed with the help of the program Statistica 9.1 (StatSoft, Inc. 2010). The conformity of data with normal distribution was verified with the aid of Shapiro-Wilk test, and the equality of variances was verified with the aid of Levene's test. The non-parametric Kruskal-Wallis method was used to test the phases of forest developmental cycle (land before afforestation, plantation, thicket, pole timber, mature stand) with respect to the number of individuals (Geotrupidae, *A. stercorosus, G. stercorarius, T. vernalis, T. typhoeus*). The forest developmental cycle was treated as an independent variable, while the number of individuals was treated as a dependent variable. The total number of individuals caught into a single trap in the course of one season of the study were treated as a sample.

RESULTS

In Człuchów Forest the representatives of the Geotrupidae family were collected in the course of the whole study period, i.e. from April till October. In total, 69389 individuals representing 5 species were collected: 31230 in 1998 and 38159 in 1999. The largest number of Geotrupidae individuals was collected at the pole timber stage (20213 specimens), while the smallest number was collected at the plantation stage (7244 specimens). As for mature stand, 18772 individuals were collected; 12340 individuals were collected in the thicket and 10820 individuals were collected on the land before afforestation. In general, taking into account the five stages of developmental cycle of pine stands, 56.2% of the total number of specimens were collected at the stages of pole timber and mature stand. The representatives of the Geotrupidae family collected in the largest numbers from pine stands in Człuchów Forest were *A. stercorosus* and *T. vernalis*. They constituted 95.6% of the total number of collected individuals (Tab. 2).

An average annual richness of Geotrupidae collected at particular stages of developmental cycle was similar. It was the highest at the pole timber stage (M=3.87, SE±0.05), and the lowest at the thicket stage (3.50 ± 0.11). At the plantation stage it amounted to 3.85 ± 0.06, at the mature stand stage it amounted to 3.75 ± 0.07 and finally, on the land before afforestation it equaled 3.77 ± 0.08 (Fig. 3). However, these disparities did not prove statistically significant.

The average richness of collected Geotrupidae were the highest at the pole timber stage (505.3 ± 26.1), and the lowest at the plantation stage (181.1 ± 6.6). In the mature stands the collection amounted to 469.3 ± 41.1 individuals, in the thicket – 308.5 ± 17.5 individuals, and on the land before afforestation – 270.5 ± 32.4 individuals (Fig. 4). The abundance of the Geotrupidae at the pole timber stage significantly differed from the abundance on the land before afforestation ($z = 5.991$, $p < 0.001$), at the plantation stage ($z = 8.113$, $p < 0.001$) and at the thicket stage ($z = 4.268$, $p <$

Table 2. The Geotrupidae collected into baited ground traps in pine stands in Człuchów Forest, 1998-1999

Species	Month	Land before afforestation	Forest plantation	Thicket stage	Pole timber stage	Mature stand	Σ	%
Anoplotrupes stercorosus (Scriba, 1791)	IV	185	128	239	630	490	**45219**	**65.2**
	V	556	288	912	2453	1893		
	VI	480	401	1558	3691	3175		
	VII	363	172	2237	3227	2606		
	VIII	551	290	1815	2832	2360		
	IX	590	427	1827	3291	3341		
	X	206	226	508	1001	270		
Geotrupes spiniger (Marsham, 1802)	IV	0	0	0	0	0	**49**	**0.1**
	V	0	0	0	0	0		
	VI	2	2	0	0	0		
	VII	15	3	0	0	0		
	VIII	22	5	0	0	0		
	IX	0	0	0	0	0		
	X	0	0	0	0	0		
Geotrupes stercorarius (Linnaeus, 1758)	IV	18	11	6	8	20	**1781**	**2.6**
	V	134	64	24	50	198		
	VI	65	23	20	73	183		
	VII	13	13	2	19	50		
	VIII	67	76	25	71	69		
	IX	65	66	34	53	107		
	X	33	28	8	46	39		
Trypocopris vernalis (Linnaeus, 1758)	IV	326	211	107	97	138	**21102**	**30.4**
	V	1090	469	416	278	372		
	VI	1563	954	662	1026	1157		
	VII	1406	623	890	471	1012		
	VIII	1780	1267	562	385	516		
	IX	988	930	364	303	566		
	X	48	64	25	19	17		
Typhaeus typhoeus (Linnaeus, 1758)	IV	62	59	10	4	9	**1238**	**1.8**
	V	106	279	27	15	24		
	VI	69	112	22	26	9		
	VII	7	8	3	1	1		
	VIII	1	1	0	2	0		
	IX	6	15	10	18	11		
	X	3	29	27	123	139		
Σ		**10820**	**7244**	**12340**	**20213**	**18772**	**69389**	**100.0**
%		**15.6**	**10.4**	**17.8**	**29.1**	**27.1**	**100.0**	

0.001). There were also confirmed differences between the collection of the Geotrupidae at the stage of maturing stand, on the land before afforestation ($z = 4.269$, $p < 0.001$) and at the plantation stage ($z = 6.391$, $p < 0.001$). Furthermore, there was confirmed the difference between the thicket stage and the plantation stage ($z = 3.845$, $p = 0.001$) ($H (4, N = 200) = 84.2830$, $p < 0.001$).

The pattern of abundance of *A. stercorosus* in particular phases of forest developmental cycle was somewhat similar. It was the highest at the pole timber stage (428.1 ± 26.1), and the lowest at the plantation stage (48.3 ± 3.5). At the stage of mature tree stand the collection of *A. stercorosus* equaled 353.4 ± 32.0 individuals, at the thicket stage – 227.4 ± 14.0 individuals, and on the land before afforestation – 73.3 ± 8.2 individuals (Fig. 5). Differences regarding the collecton of *A. stercorosus* were significant between the pole timber stage and the land before afforestation ($z = 8.914$, $p < 0.001$), forest plantations ($z = 9.819$, $p < 0.001$) and the thicket ($z = 3.894$, $p < 0.001$). The differences were also significant between the maturing stand and the land before afforestation ($z = 7.042$, $p < 0.001$) as well as the plantations ($z = 7.947$, $p < 0.001$). Furthermore, a significant difference was also discovered betwen the thicket and the land before afforestation ($z = 5.019$, $p < 0.001$) as well as the plantations ($z = 5.924$, $p < 0.001$) ($H (4, N = 200) = 149.002$, $p < 0.001$).

The highest average abundance of *T. vernalis* was observed on the land before afforestation (180.0 ± 24.5), while the lowest was observed at the plantation stage (113.0 ± 4.4) and at the stage of mature stand (94.5 ± 7.7). It was also clearly lower at the thicket stage (75.7 ± 5.0) and pole timber stage (64.5 ± 3.3) (Fig. 6). Significant differences were discovered between the collection of *T. vernalis* on the land before afforestation and the thicket stage ($z = 3.928$, $p < 0.001$) as well as

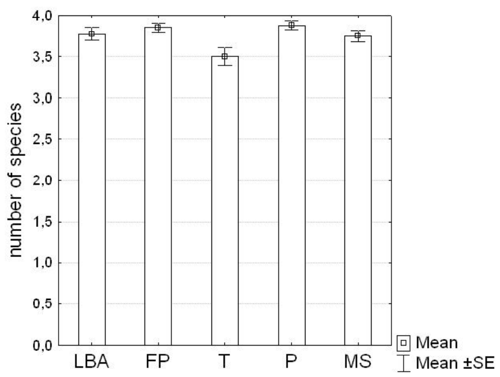

Fig. 3. Average annual species richness of Geotrupidae species in pine stands in Człuchów Forest, 1998-1999 (MS – mature stand, P – pole timber, T – thicket, FP – forest plantation, LBA – land before afforestation, SE – standart error)

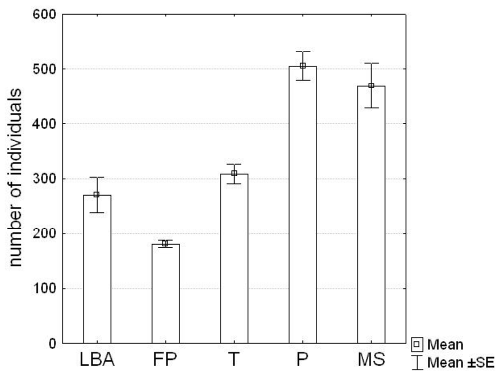

Fig. 4. Average annual abundance of the Geotrupidae in pine stands in Człuchów Forest, 1998-1999 (explanations as in Fig. 2)

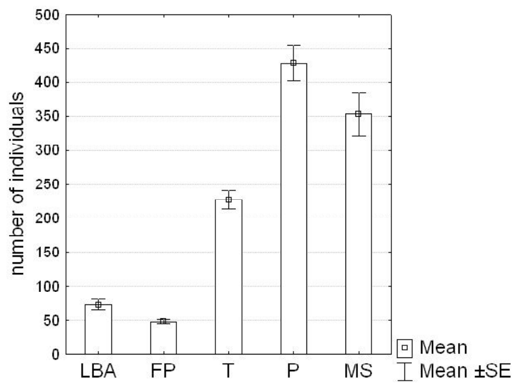

Fig. 5. Average annual abundance of *A. stercorosus* in pine stands in Człuchów Forest, 1998-1999 (explanations as in Fig. 2)

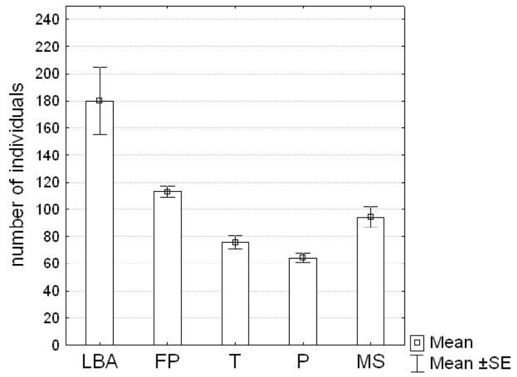

Fig. 6. Average annual abundance of *T. vernalis* in pine stands in Człuchów Forest, 1998-1999 (explanations as in Fig. 2)

the pole timber stage ($z = 5.469$, $p < 0.001$). Furthermore, significant differences were observed between the plantation stage and the thicket stage ($z = 4.240$, $p < 0.001$), as well as the pole timber stage ($z = 5.781$, $p < 0.001$). Finally, a significant difference was discovered between the stage of mature stand and the plantation stage ($z = 2.889$, $p = 0.037$) as well as the pole timber stage ($z = 2.881$, $p = 0.040$) ($H (4, N=200)=49.765$, $p < 0.001$).

The average abundance of *G. stercorarius* was definitely the highest in mature stands (16.7 ± 1.8), lower on the land before afforestation (9.9 ± 1.1), at the pole timber stage (8.0 ± 0.8) and the plantation stage (7.0 ± 1.0), while at the thicket stage it was the lowest (3.0 ± 0.4) (Fig. 7). The differences regarding the collection of *G. stercorarius* were statistically significant between the stage of mature stand and all the remaining stages of the forest developmental cycle: land before afforestation ($z = 2.914$, $p = 0.036$), plantation stage ($z = 4.650$, $p < 0.001$), thicket stage ($z = 7.869$, $p < 0.001$) and pole timber stage ($z = 3.682$, $p = 0.002$). Furthermore, a significant difference was also discovered between the thicket stage and all of the following: land before afforestation ($z = 4.955$, $p < 0.001$), plantation stage ($z = 3.219$, $p = 0.013$) and pole timber stage ($z = 4.187$, $p < 0.001$) ($H (4, N = 200) = 65.282$, $p < 0.001$). *G. spiniger* was collected solely on the land before afforestation (1.0 ± 0.2) and at the plantation stage (0.3 ± 0.1).

The average abundance of *T. typhoeus* was definitely the highest at the plantation stage (12.6 ± 2.5), and the lowest at the thicket stage (2.5 ± 0.4). In the remaining phases of the forest developmental stages the collection of the species was similar. On the land before afforestation it equaled 6.4 ± 1.6 individuals, at the pole timber stage – 4.7 ± 0.7, and at the stage of mature stand – 4.8 ± 1.0 (Fig. 8). Differences in the collection of *T. typhoeus* were significant between the plantation stage and the land before afforestation ($z = 3.682$, $p = 0.002$), as well as the thicket stage ($z = 4.208$, $p < 0.001$) ($H (4, N = 200) = 21.792$, $p < 0.001$).

The collection of the Geotrupidae in pine stands in Człuchów Forest, as well as the collection of the most abundant representative of this family, namely *A. stercorosus*, grew from the plantation stage until the pole timber stage and then decreased at the stage of the mature stand. As for the collection of *T. vernalis*, it decreased from the first phase of the forest developmental cycle until the pole timber stage, and then increased at the stage of the mature stand. The collection of *G. stercorosus* decreased from the stage of the land before afforestation, achieving its lowest value at the thicket stage, and to increase again as the tree stand matured. *G. spiniger* was col-

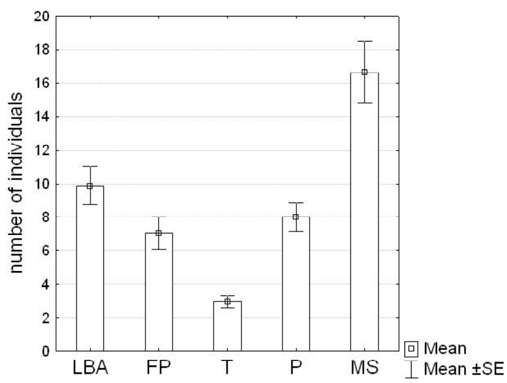

Fig. 7. Average annual abundance of *G. stercorarius* in pine stands in Człuchów Forest, 1998-1999 (explanations as in Fig. 2)

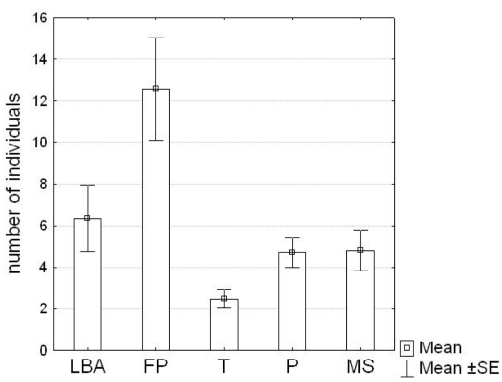

Fig. 8. Average annual collection of *T. typhoeus* in pine stands in Człuchów Forest, 1998-1999 (explanations as in Fig. 2)

lected solely on the land before afforestation and in the plantations. The collection of *T. typhoeus* grew from the stage of the land before afforestation and achieved the peak of abundance at the plantation stage, only to become dramatically reduced and retain a similar level at the older stages of forest development (Figs. 9a,b).

The PCA analysis of Geotrupidae communities showed the preference of particular species for various phases of the developmental cycle of pine stands. The studied axes of the graph were described by eigenvalues: 0.996, 0.030 for the first two axes. The cumulative percentage of variance of species for the the first axis is 99.6%. From the left to the right side of the PCA diagram there were featured: thicket (T) and older stages of tree stands in the following order: pole timber (P) and mature stand (MT), followed by the land before afforestation (LBA) and forest plantation (FP). This suggested the succession gradient from the land before afforestation (the right side of the diagram) to the forest areas with stands at various stages of development (the left side). As for the vertical axis, it seemed that it might display the gradient of the thickness of humus layer. In the upper part of the diagram there were located the tree stands with a rich humus layer, while in the lower part of the diagram there were located the pole timber wood with a poor humus layer and the land before afforestation with post-agricultural soil structure. The presence of such forest species as *A. stercorosus* and *T. vernalis* correlated with the first axis; the first of these species was associated with older trees stands while the latter – with younger ones (Fig. 10).

Two autonomous faunistic agglomerations were distinguished using cluster analysis (Fig. 11). In one of these agglomerations the role of a superdominant was played by *T. vernalis* (64.9%), while the role of a dominant was played by *A. stercorosus* (26.9%). The subdominants included

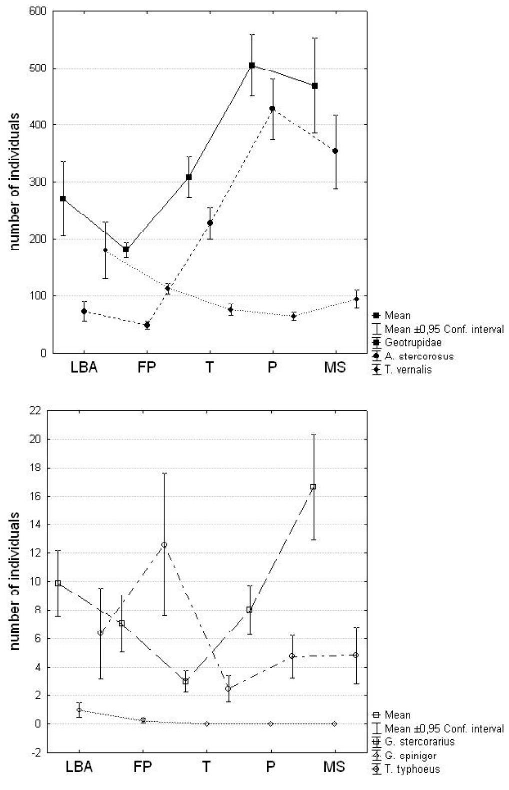

Fig. 9a,b. Average annual abundance of Geotrupidae and particular species collected into a baited ground trap in Człuchów Forest, 1998-1999 (MS – mature stand, P – pole timber, T – thicket, FP – forest plantation, LBA – land before afforestation)

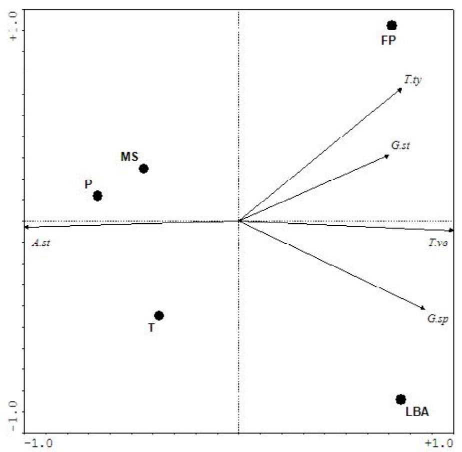

Fig. 10. A diagram of PCA analysis illustrating the dominance structure in Geotrupidae communities inhabiting various phases of the developmental cycle of pine stands in Człuchów Forest, 1998-1999 (explanations as in Fig. 9)

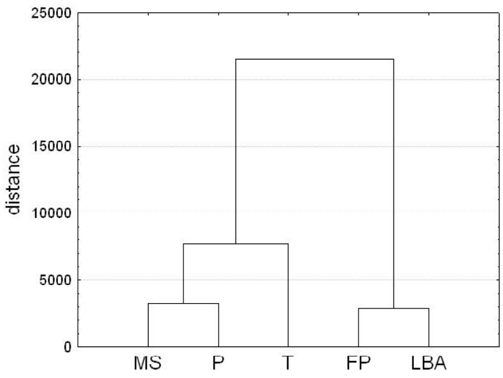

Fig. 11. A dendrogram of similarity for Geotrupidae communities inhabiting various phases of the developmental cycle of pine stands in Człuchów Forest, 1998-1999 (explanations as in Fig. 9)

T. typhoeus (4.2%) and *G. stercorosus* (3.7%), with *G. spiniger* (0.3%) as an accesory species. Another agglomeration comprised the communities inhabiting such stages as: thicket, pole timber and mature stand, with *A. stercorosus* (78.6%) in the role of a superdominant and *T. vernalis* (18.3%) in the role of a dominant. The subdominant species was *G. stercorosus* (2.2%), with *T. typhoeus* (0.9%) as an accessory species. Two groups were further differentiated within this agglomeration, one of which included the community inhabiting the thicket stage and the other which comprised the Geotrupidae communities encountered at the stages of pole timber and mature stand (Fig. 11).

DISCUSSION

The data displays the differences in both abundance and species composition of Geotrupidae communities inhabiting younger and older phases of the pine stand developmental cycle. More abundant communities of the Geotrupidae are encountered at the pole timber stage and the stage of mature stand in comparison with the land before afforestation (brownfields adjoining to a forest, clear-cut areas) and forest plantations. *A. stercorosus* and *T. vernalis*, which at the larval stage feed on the partly decomposed plant litter together with faeces of small mammals it contains, as well as the faeces of large animals, if available, are both forest species; the latter one ought to be considered a forest generalist. By digging tunnels and bringing plant litter underground they contribute to soil fertilization. In pine stands in Człuchów Forest these beetle species constitute the hard core of Geotrupidae communities. According to the study by Szyszko (1983a), *A. stercorosus* is the most abundant of all species reprsenting the superfamily *Scarabaeoidea*. In open areas of Central Europe the abundance of the Geotrupidae is decreasing to the advantage of species belonging to the family Scarabaeidae (Sowig & Wassmer 1994, Wassmer 1995, Bunalski 1996, Górz 2007). In La Mandria Park in north-eastern Italy, which constitutes a mosaic of forests and open areas, the Scarabaeidae (including Aphodiinae 32.5%) constitute 94% of the community of coprophagous Scarabaeoidea, while the Geotrupidae constitute just 6%. In this area *A. stercorosus* clearly prefers forest areas (Barbero et al. 1999). At the same time, the umbrophilous *A. stercorosus* clearly prefers middle-aged and older tree stands, while the helophilous *T. vernalis* prefers young tree stands and finds optimum conditions for development at the stage of forest plantation. Both species play an enormous role in the process of changing post-agricultural soil into forest soil. By penetrating the brownfields in the proximity of forests, by digging tunnels and buring feaces of wild animals as well as fallen leaves, they alter the structure and properties of post-agricultural soil. Another forest species, namely *T. typhoeus*, inhabits moors and pine forests growing on sandy soil, where it feeds on the droppings of rabbits, as well as the feaces of deer, roe deer and sheep, and, though somewhat less frequently, also the feaces of horses and cows (Brussaard 1983, Burakowski et al. 1983, Hetmański et al. 2009). In Poland it has been recorded in dispersed localities, mainly in the western part of the country, and the range of its occurrence strongly coincides with the range of a wild rabbit (Szujecki 1983). According to Bunalski (1996), the range of its distribution in Poland coincides with the influence of Atlantic climate. Within the investigated area it is a common species, with two clear peaks of abundance in late spring and in autumn. It has been identified as a permanent member of Geotrupidae communities inhabiting pine stands in Człuchów Forest. The presence of beetles representing this species have been observed in clear-cuts and at all stages of forest development; it has been collected in the largest numbers in forest plantations. *G. stercorarius* is a common species within the whole area of Poland, feeding on horse faeces (Burakowski et al. 1983). The studies have proved its eurytopic character. In Człuchów Forest it has been identified as a permanent element of Geotrupidae communities inhabiting pine stands. *G. spiniger* can be found locally in dry pastures and in sandy, sunny brownfields, where it feeds on faeces (Burakowski et al. 1983). Wassmer (1995), having analyzed the structure of communities of the coprophagous Scarabaeoidea on a meadow in the neighborhood of Freiburg in Germany, identified this species as a silvicole. In the course of the research conducted in Człuchów Forest, *G. spiniger* was ecnountered only in brownfields adjoining the forests and the pine plantation growing on post-agricultural land, which has confirmed its preferences regarding open areas (praticole). The rare local species *G. mutator* was not collected in the course of the field study. This species prefers open areas, can be found on meadows along rivers, in the proximity of midfield clump of trees, and on the outskirts of tree stands.

Summing up the obtained results, it can be stated that in the pine stands in Człuchów Forest, the *Geotrupidae*, and *A. stercorosus* are the most abundant at the pole timber stage followed by the stage of mature stand. Another abundant representative of this family, *T. vernalis*, clearly prefers the land before afforestation and forest plantations; it does not avoid mature stands either. *G. stercorosus* is the most abundant in mature stands and on the land before afforestation; it also penetrates forest plantations and can be found in a pine stand at the pole timber stage. At the same time, *G. spiniger* inhabits solely the land before afforestation and occasionally appears also in forest plantations. *T. typhoeus*, even though it can be encountered at all stages of the forest developmental cycle, it clearly prefers to inhabit forest plantations.

It can be observed, while analyzing the domination structure of Geotrupidae communities inhabiting pine forests, that two types of communities are present. One type of community inhabits the land before afforestation and forest plantations; these are heliophilous Geotrupidae communities of pine forests. The other type can be encountered at the stages of thicket, pole timber and mature stand; these are umbrophilous Geotrupidae communities of pine forests. The basic factor which allows to distinguish one type from another is the presence of either *T. vernalis* or *A. stercorosus* in the role of a superdominant. The heliophilous Geotrupidae communities of pine forests are characterized by the fact that the role of the superdominant is played by *T. vernalis* and *G. spiniger* is present. In such a community *A. stercorosus* is a dominant species, and the subdominant ones are *T. typhoeus* and *G. stercorarius*. According to Klimaszewski & Szyszko (2000), the average collection of *T. vernalis* in forest areas is negatively correlated with forest cover. In Człuchów Forest, the collection of *T. vernalis* became lower at the thicket stage, while the collection of *A. stercorosus* at this stage became higher. The average share of *T. vernalis* in Geotrupidae communities inhabiting forest plantations equaled 36.6% and became reduced to 24.5% at the thicket stage, while at the same development stages the average share of *A. stercorosus* increased from 15.7% to 73.7%, respectively. At the thicket stage, because the tree crowns exapand and the soil becomes fully shaded, the characteristic sylvan microclimate develops under the canopy of the trees. At the same time, the growing thickness of the litter layer is conducive to the appearance of shade-loving and saprophagous species of the Geotrupidae. The quicker the tree crowns expand, the quicker the Geotrupidae community characteristic of mature developmental stages of the forest will appear. Umbrophilous Geotrupidae communities in pine forests are characterized by the presence of *A. stercorosus* as a superdominant and the absence of *G. spiniger*. Szyszko (1983) observed that in forest areas *A. stercorosus* was collected in the largest numbers in 60-year-old tree stands. In this type of community *T. vernalis* is a dominant species, with *G. stercorarius* as a subdominant one, while *T. typhoeus* becomes an accessory species.

The abundance of *A. stercorosus,* the most abundant species in the Geotrupidae community inhabiting pine stands in Człuchów Forest, grew as the pine stands matured, until they reached the stage of mature stand. Then the abundance of the species became slightly reduced, probably in connection with the fact that at this stage the canopy was not impenetrable to sunlight anymore, and the sunlight could reach the forest bottom. The abundance of the second most numerous species in the community, namely *T. vernalis*, decreased as the pine stands matured until it finally began to increase at the stage of mature stand. The abundance of the other three species composing the Geotrupidae communities inhabiting pine stands was low, especially regarding the dominant species of *A. stercorosus* and *T. vernalis*. As a result, the abundance of Geotrupidae communities at particular stages of pine stand development reflected the trend governing the abundance of *A. stercorosus*, which was the most abundant representative of the family Geotrupidae in forest environment. The numbers of Geotrupidae collected at the pole timber stage differed considerably from the numbers collected on the land before afforestation, as well as at the stages of plantation and thicket. There was also confirmed the difference between the collection of the Geotrupidae in maturing stands in comparison with the stage of plantation, as well as the difference between the thicket stage and the plantation stage. Hence, it seems that the hypothesis that the abundance of Geotrupidae communities grows as the tree stands mature has been confirmed. As for the hypothesis that the number of species composing the Geotrupidae communities becomes reduced as the pine stands mature, it ought to be rejected. The differences in the number of species present at particular development stages turned out to be insignificant. The evaluation of species preferences with respect to particular phases of the developmental cycle of pine stands, performed by implementing the PCA method, as well as the evaluation of faunistic similarity among the Geotrupidae communities inhabiting various stages of the forest developmental cycle, performed with the aid of the numeric cluster analysis utilizing Ward's method, have proved that there did exist differences in the species composition between communities inhabiting forest plantations, thickets and tree stands of older age classes.

CONCLUSIONS

- The structure of Geotrupidae communities inhabiting pine stands changes in the course of the forest developmental cycle.
- The abundance of Geotrupidae communities grows as the pine stands mature, increasing from the stage of forest plantations until the pole timber stage, and then decreasing again in mature stands.
- The number of species comprising a community of the Geotrupidae does not undergo significant changes as the pine stands mature, but there can be observed changes in species composition.
- Brownfields adjoining to forests, clear-cut areas and forest plantations were inhabited by heliphilous communities of Geotrupidae typical of pine forests, with *T. vernalis* as a superdominant.
- Thicket, pole timber and mature stands were inhabited by umbrophilous Geotrupidae typical of forests, with *Anoplotrupes stercorosus* (Scriba, 1791) as a superdominant.
- As the forest bottom was gradually shaded when the crowns of young trees developed, the species *G. spiniger*, characteristic of open spaces, was „replaced" by the forest species *T. typhoeus*.

ACKNOWLEDGEMENTS

I would like to thank Mr J. Skłodowski (Warsaw) for his valuable remarks and advice given me throughout the study.

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Received: 01.10.2011.
Accepted: 20.12.2011.