Baltic J. Coleopterol. 7(1) 2007
ISSN 1407 - 8619

Ground beetle assemblages (Coleoptera, Carabidae) in the third year of regeneration after a hurricane in the Puszcza Piska pine forests*

Jarosław Skłodowski, Paulina Garbalińska

Skłodowski J., Garbalińska P. 2007. Ground beetle assemblages (Coleoptera, Carabidae) in the third year of regeneration after a hurricane in the Puszcza Piska pine forests. *Baltic J. Coleopterol. 7(1): 17 - 36.*

In 2002, pine forests in Pisz Forest District (north-eastern Poland) were disturbed by a hurricane. Since then a survey on ground beetle (Coleoptera: Carabidae) assemblages inhabiting the damaged stands has been carried out. This article presents the results of the third year of this study. The carabid beetle fauna of damaged stands was compared with that of non-damaged stands in the Maskulińskie Forest District. In both disturbed and control stands, 15 plots in five different age classes were distinguished and investigated (3 plots in each age class): class I (20-40 years old), class II (40-50 years old), class III (50-60 years old), class IV (60-70 years old) and class V (above 70 years old). Beetles were sampled using modified pitfall traps. The soil CO_2 efflux rate and C/N ratio of soil were also measured. A total of 5115 carabid individuals representing 38 species were recorded. After the hurricane, *Carabidae* assemblages markedly declined in abundance, although species richness was significantly higher in damaged stands compared to control stands (32 species and 26 species respectively). Both Ward˙s cluster analysis and CCA analysis clearly distinguished between carabid assemblages inhabiting disturbed stands and non-disturbed ones. Windthrow considerably reduced the proportion of forest, European and autumn breeding species fauna in carabid assemblages. A marked decline in abundance of hygrophilous species in favour of xerophilous ones was also observed. *Amara* and *Harpalus* species responded positively to disturbance increasing in abundance and richness in stand openings. According to the SPC (Sum of Progressive Characteristics) index reduction in Pisz Forest District, it might be concluded that the regeneration of carabid beetle assemblages in stands damaged by the hurricane has not started yet.

Key words: Ground beetles, carabid beetles, Carabidae, hurricane, disturbances, regeneration succession, windbreak, windthrow

Jarosław Skłodowski, Paulina Garbalińska. SGGW, Warsaw Agricultural University, Dept. of Forest Protection and Ecology, Nowoursynowska 159, 02-776 Warszawa, Poland

* Financial support of Ministry of Science and Higher Education - project number 2PO6L02626.

Introduction

Natural disturbances, including fires, hurricanes and pest outbreaks, as well as species responses to them, are considered to be essential components of ecosystem function (Bengtsson *et al.*, 2000; Chapin *et al.*, 2002; Niemelä, 1999; Pascarella *et al.*, 2004; Pickett & White, 1985; Pickett *et al.*, 1999; Pontailler *et al.*, 1997; Wolf *et al.*, 2004). The scale of disturbance may vary considerably between different forest types (Bengtsson *et al.*, 2000). Forest fires covering vast areas are typical disturbance elements of boreal and Mediterranean forest ecosystems in particular, whereas temperate forest dynamics are characterised rather by windthrows, small-scale gap dynamics and, to some extent, the impact of large herbivores foraging (Bengtsson *et al.*, 2000; Faliński, 1986; Linder & Östlund, 1998; Wolf *et al.*, 2004; Zackrisson, 1977).

The disturbance caused by the hurricane is very intensive for a brief period of time, though the subsequent succession and recovery is slow and profound. The early phase of this succession is characterised by increased tree mortality and the creation of a mosaic of gaps characterised by large amounts of sun-exposed coarse woody debris and a drier and more variable microclimate (Bouget, 2005a; Bouget & Duelli, 2004; Pascarella *et al.*, 2004). Litter accumulation and soil nutrient content, as well as understory vegetation dynamics (Bouget, 2005a; Bouget & Duelli, 2004; Pascarella *et al.*, 2004; Ulanova, 2000), are also significantly affected. Therefore, windthrows play an important role in forest dynamics and succession, and create a variety of environmental resources which are of vital importance for the persistence of many species, especially invertebrates (Bouget, 2005a, 2005b; Bouget & Duelli, 2004; Kaila *et al.*, 1997; Lindhe *et al.*, 2004; Lindhe & Lindelöw, 2004).

However, there is still little information on the responses of invertebrate assemblages, such as the soil macrofauna, to hurricane damaged forest stands. Responses of ground beetle communities to windthrow disturbance have been reported by Bouget (2005) and Duelli *et al.* (2002). Bouget (2005b) and Bouget & Duelli (2004) have also investigated the saproxylic insect fauna of stands destroyed by a hurricane. Still relatively few surveys seem to have been carried out on long-term effects of windthrow on epigeic beetle communities. Significantly more attention has been paid to changes in soil arthropod communities subjected to anthropogenic disturbances, comprising clear-cutting on different scales and other forest management practices (Koivula, 2001; Koivula *et al.*, 2002; Pihlaja *et al.*, 2006; Skłodowski, 1995a, 1995b, 2001a, 2002, 2006; Szyszko, 1983; Szujecki *et al.*, 1983).

In July 2002, pine forests in Puszcza Piska, Puszcza Borecka and Puszcza Kurpiowska (north-east Poland) were hit by a hurricane. In total 33 000 ha of forest stands were destroyed, as windthrows, uprooted or partially fallen trees in an area 130 km long and 12 km wide. Most of the killed and damaged trees were quickly removed and the area was reforested. However, 445 ha of disturbed stand in the Pisz Forest District ("Szast Forest") was left untouched and set aside as an experimental area providing an opportunity to monitor the regenerative succession. Since spring 2003, the Department of Forest Protection, Ecology and Ecotourism has been carrying out a survey of the ground beetle (Col. Carabidae), spider, Diplopoda, Collembola and dung beetle (*Geotrupes stercorosus* and *G. vernalis*) assemblages inhabiting this area. Environmental factors comprising soil CO_2 efflux rate, C/N ratio of soil, soil pH, organic matter decomposition rate and leaf area index (LAI), were also included in the survey.

Carabid beetles are considered by many authors to be valuable environmental indicators, as they are a highly diverse and taxonomically well known group (Bouget, 2005a; Poole *et al.*, 2003, Niemelä *et al.*, 1993a; Szyszko, 1983). Moreover, they are sensitive to changes of environmental factors, such as temperature, moisture, soil and vegetation cover (Bouget, 2005a; Ings & Hartley, 1999; Poole *et al.*, 2003; Skłodowski, 2002, 2006; Szyszko, 1983). In addition, these beetles may be easily sampled using pitfall traps (Ings & Hartley, 1999; Poole *et al.*, 2003).

Hurricane influences on the carabid assemblage were evident already in the first year following disturbance. Carabid assemblages inhabiting affected stands declined in abundance in comparison with corresponding assemblages in control stands. After the windthrow, open habitat species, including representatives of *Amara* and *Harpalus,* were recorded. The proportion of xerophilous individuals in carabid assemblages increased, with a corresponding decrease in forest and hygrophilous species (Skłodowski & Zdzioch 2005a, 2005b). Moreover, the proportion of large zoophages in Carabidae assemblages observed in mature stands (> 70 years old) affected by the hurricane, was lower than in assemblages of corresponding control stands (Skłodowski & Zdzioch 2005a, 2005b).

In the second year, the changes in the carabid assemblages inhabiting these stands were even more pronounced. The overall abundance of Carabidae decreased significantly. Furthermore, the proportion of large zoophages, forest species and hygrophilous species, was profoundly reduced in favour of xerophilous and open-land species, including *Amara* sp. and *Harpalus* sp. (Skłodowski & Zdzioch 2006). Considerable changes in environmental characteristics of the affected stands were also observed. Opening of the canopy apparently resulted in a significant reduction in the organic matter layer and contributed to moss cover degeneration (Sławski 2007; Skłodowski & Buszyniewicz 2007). Additionally, in windthrow gaps vigorous regeneration of pine and birch was observed (Skłodowski & Zdzioch 2006).

In 2005 the survey was continued with the aim at tracing the further succession of these carabid assemblages.

Material and methods

Study area

Sampling of carabids and environmental research were carried out at study sites that had been set after the hurricane in 2003. These sites comprised forest stands affected by the hurricane located in Pisz Forest District – "Szast Forest" (referred to as site "P") and non-damaged control stands in Maskulińskie Forest District – "Zaroślak Forest" (referred to as site "M"), in the north-east region of Poland. Both study sites were classified as coniferous forests – low fertility habitats with a predominance of *Pinus sylvestris* and *Picea abies* on mesic (fresh) habitat type (no inundation at any time of the year). At each site the following stand age classes were selected for investigation: class I (comprising stands 20-40 years old), class II (stands 40-50 years old), class III (stands 50-60 years old), class IV (stands 60-70 years old) and class V (stands > 70 years old). Three research plots were set up in stands of each of the distinguished age classes, making a total of 30 research plots in the two districts.

Carabid sampling

The beetles were continuously sampled over a 6 month period (May - October) using modified pitfall traps (Barber˙s traps). Each trap consisted of 10 cm diameter 0.5 l glass jar filled with 100 ml 70% ethylene glycol to kill and preserve the trapped insects and set into the ground up to its upper edge. A plastic funnel (12 cm in diameter) was put on each of the jars to extend the trap˙s catching range and to prevent small vertebrates from falling into it. Additionally each of the traps was covered with a roof (wooden square 20 cm x 20 cm placed approximately 5 cm above each trap) in order to avoid inundation of the jar with rain. Five pitfall traps were installed in each plot 10 m apart and emptied 4 times, at 6-week intervals.

Site characteristics

Soil samples were also collected from the mineral layer at 10 cm depth in 3 replicates: 29 (IV) April, 5 (VII) August and 24 (X) November from each site. For each sample, an analysis of carbon and nitrogen content was conducted by the authorised laboratory: SGGW Analytic Centre. In addition, the soil CO_2 efflux rate was measured directly in the field using a Gazex meter, which compared the air sample in infra-red radiation to the control one with the accuracy of ppm units.

Data analysis

All collected carabid beetles were identified to species level and measured with an accuracy of ± 0.5 mm. The body lengths obtained were subsequently transformed to biomass, according to the formula proposed by Szujecki *et al.* (1983). For statistical analysis, all carabid beetles caught were classified according to the following criteria: (1) zoogeographical, (2) environmental, (3) trophic and (4) developmental. This classification was based on literature (Burakowski *et al.* 1973, 1974; Larson 1939; Szyszko 1983; Szujecki *et al.* 1983; Turin 2000). The zoogeographical groups distinguished were: Palaearctic, Holarctic and European. The European species have a more limited geographical range and are regarded as more stenotopic in comparison to the previous groups. On the basis of environmental criterion, carabid beetles were grouped as: forest species (restricted to forest habitats and reproducing there, hardly ever or never observed outside forest stands), open-habitat species (recorded mostly in open areas and canopy gaps) or eurytopic species (able to thrive both in forested and open areas). Regarding to trophic preferences, the three following groups were distinguished: hemizoophages (partially herbivorous, comprising mostly *Amara, Bradycellus* and *Harpalus* species), small zoophages (predators with a biomass of less than 100 mg) and large zoophages (predators whose biomass exceeds 100 mg). According to Larson (1939) Carabidae were divided into spring breeding species (ovipositing in spring, overwintering in the stage of imago) or autumn breeding species (ovipositing in summer, overwintering usually as larvae). Beetles assigned to the criteria forest species, European species, large zoophages or autumn breeders group are regarded as characteristic of mature and undisturbed forest stands (Szyszko 1983; Szujecki *et al.* 1983; Skłodowski 1995a, 1995b, 2002).

Additionally carabids were classified as hygrophilous or xerophilous, according to their preference for habitat humidity. A prevalence of hygrophilous species in assemblages may indicate either a high moisture level or shading by the closed canopy.

The sum of biomasses of all individuals in an assemblage was subsequently divided by their abundance, in order to obtain the Mean Individual Biomass (MIB) index (Szyszko 1983, 2002), the values of which are positively correlated with stand age and naturalness. The Sum of Progressive Characteristics (SPC) index (Skłodowski 1997) was also used in this study with the aim of describing the successional stage of carabid assemblages. The SPC index summarizes the proportion of: large zoophages, autumn breeders, forest species and European species individuals in the whole Carabidae assemblage. It may thus theoretically reach a maximum value of 400 units (4 x 100%), however the highest observed value was about 350 units. As the above mentioned groups are prevalent in mature and undisturbed forests, the SPC index value is significantly positively correlated with the age of the stand in question [r = + 0,93, p = 0,0001, n =76; Skłodowski (1997)] and is calculated as follows:

*SPC = 74.9 + 102 * LOG (stand age)*

The two values are coefficients: 74.9 for the model intercept and 102 for the regression slope.

The statistical analysis was conducted using STATISTICA [STATISTICA; StatSoft, Inc. (1997)]. The data obtained were tested for normality of distribution with the Shapiro-Wilk˙s statistic. In order to verify the differences between carabid assemblages studied, 2-way ANOVA was used with stand age and stand damage as variables. A *post-hoc* comparison of significant differences was confirmed using the LSD (least significant difference) *post-hoc* test. Species-composition similarities of carabid assemblages were investigated using Ward˙s cluster analysis, based on Euclidean distance as a similarity measurement. Whitaker plots of log abundance on species rank were also used (Krebs 1999). In attempt to explain the pattern of variation in Carabidae assemblages, as well to identify the environmental variables affecting species composition and structure of these assemblages, a Canonical Correspondence

Analysis (CCA) was carried out using the CANOCO software (ter Braak & Smilauer 1997).

Results

Sample overview

In the third year of the study, a total of 5115 carabid individuals representing 38 species were caught. The most abundant species from both the Pisz and Maskulińskie study sites were: *Carabus arcensis* (847 individuals in P stands and 712 individuals in M stands) and *C. violaceus* (334 and 328 individuals respectively). Additionally in Maskulińskie Forest District *Calathus micropterus* (556 individuals), *Pterostichus niger* (708 ind.) and *P. oblongopunctatus* (527 ind.) were numerously recorded (Tab. 1). Overall these 5 prevailing species made up 78.5% of the total yield.

Effect of hurricane on carabid abundance and species richness

As in the first two years of the study, the differences in Carabidae abundance and richness between disturbed and unaffected stands recorded in 2005 were profound. Carabid beetles significantly declined in abundance after the hurricane, as the total number of individuals caught and the mean number of individuals caught per trap recorded in the Pisz Forest District (1829 individuals and 24.4 ind/trap) were markedly lower than in Maskulińskie Forest District (3286 and 43.8 respectively – Table 1).

The opposite trend was observed for species richness. The total number of species caught increased after the disturbance (32 species recorded in destroyed P stands vs. 26 species yielded in control M stands – Tab. 1), although the mean number of species caught per trap was slightly lower in stands damaged by the hurricane (5.5 sp/trap) compared to control stands (6.8 sp/trap).

Effect of hurricane on the structure of carabid assemblages

Cluster analysis clearly separated carabid assemblages inhabiting stands affected by the hurricane (P) from those of non-affected (M) ones (Fig. 1).

Significant faunal differences between both stands types were also indicated using Whittaker plots. According to this analysis, disturbed stands were characterised by higher dominance indices than control stands, with the most pro-

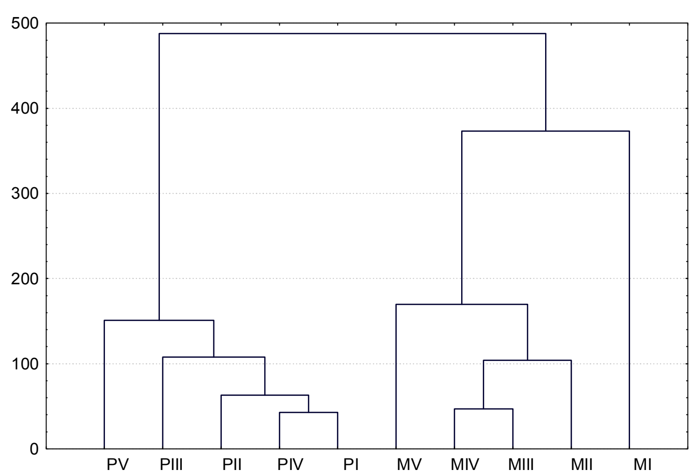

Fig. 1. Cluster analysis for the carabid beetle assemblages inhabiting stands affected by the hurricane (P) and control stands (M) in age classes I-V. Ward's method, Euclidean distance.

Table. 1. List of carabid beetle species caught in pitfall traps in stands affected by the hurricane (P) and in control stands (M) in age classes I - V.

No.	Species	PI	PII	PIII	PIV	PV	MI	MII	MIII	MIV	MV
1.	*Acupalpus brunnipes* (Sturm, 1825)			1							
2.	*Agonum fuliginosus* (Duftschmid, 1812)							1			
3.	*Amara aenea* (De Geer, 1774)		2		1	3					
4.	*A. brunnea* (Gyllenhal, 1810)		1								
5.	*A. communis* (Panzer, 1797)					1					
6.	*A. consularis* (Duftschmid, 1812)					1					
7.	*A. lunicollis* Schiodte, 1837	6	15	23	32	52		1		1	
8.	*Calathus erratus* (C.R.Sahlberg, 1827)	4		1		2		4	1		
9.	*C. melanocephalus* (Linnaeus, 1758)							1			
10.	*C. micropterus* (Duftschmid, 1812)	8	15	24	21	37	321	63	26	55	91
11.	*Carabus arcensis* Herbst, 1784	175	126	113	175	258	138	174	96	116	188
12.	*C. convexus* Fabricius, 1775										2
13.	*C. coriaceus* Linnaeus, 1758						66	72	44	22	68
14.	*C. glabratus* Paykull, 1790	2	2	2		2	11	2	4	1	6
15.	*C. granulatus* Linnaeus, 1758				1	2					
16.	*C. hortensis* Linnaeus, 1758	1	2	2	1	9	7	6	10		8
17.	*C. nemoralis* O.F. Muller, 1764	1	1	1	1		1	1	1		3
18.	*C. violaceus* Linnaeus, 1758	65	43	121	49	56	60	98	63	50	57
19.	*Cychrus caraboides* (Linnaeus, 1758)	2	1	1		1	5	12	7	6	6
20.	*Cymindis vaporariorum* (Linnaeus, 1758)		1					1		1	
21.	*Harpalus affinis* (Schrank, 1781)					1					
22.	*H. latus* (Linnaeus, 1758)	1			3	1		1			
23.	*H. quadripunctatus* Dejean, 18*29*	1		2		1					1
24.	*H. rufipes* (de Geer, 1774)	4	4	3	6	6					
25.	*H. rufitarsis* (Illiger, 1778)		2	2		1					
26.	*H. tardus* (Panzer, 1797)						1				
27.	*Notiophilus biguttatus* (Fabricius, 1799)		2	1							
28.	*N. germinyi* Fauvel in Grenier, 1863	1		1	1	1					
29.	*Pterostichus aethiops* (Panzer, 1797)				1	1	3	3	1	1	2
30.	*P. caerulescens* (Linnaeus, 1758)	22	6	7	6	5	9	9	7	6	20
31.	*P. cupreus* (Linnaeus, 1758)	1				3	1		1		
32.	*P. diligens* (Sturm, 1824)						1				
33.	*P. melanarius* (Illiger, 1798)	1					2				
34.	*P. niger* (Schaller, 1783)	12	13	12	45	46	122	141	120	121	204
35.	*P. oblongopunctatus* (Fabricius, 1787)	23	26	16	31	32	128	92	60	88	159
36.	*P. vernalis* (Panzer, 1796)		1							1	
37.	*P. virens* (O.F.Muller, 1776)	1				4					3
38.	*Synuchus nivalis* (Illiger, 1798)			1		1					
Total number of individuals		331	263	334	374	527	876	682	441	469	818
Total number of species		19	18	19	15	25	16	18	14	13	15

nounced differences recorded for the oldest stands (Fig. 2). This was because the carabid assemblages of affected stands were characterised by a considerable (almost 50%) predominance of a single species, namely *Carabus arcensis,* accompanied by low (even less than 10%) contribution of subdominants.

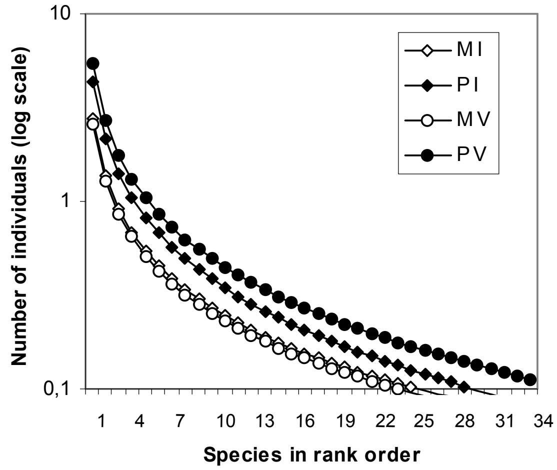

Fig. 2. Log-fitted abundance curves for carabid beetle species abundance in stands destroyed by the hurricane (P) and control stands (M) in age classes: I and V.

Significant differences in structure of carabid assemblages inhabiting disturbed and non-disturbed stands of different age classes were confirmed by the 2-way ANOVA test.

A significant (LSD test $p < 0.001$) 11-17% reduction in the proportion of forest species individuals in carabid assemblages of destroyed stands in comparison with control stands was observed (Fig. 3, Tab. 2). Some of the forest species caught on non-affected sites were absent from the disturbed stands (e.g. *Carabus coriaceus*). However, no significant differences in the proportion of forest species individuals were recorded for stands of any particular age class (Tab. 2).

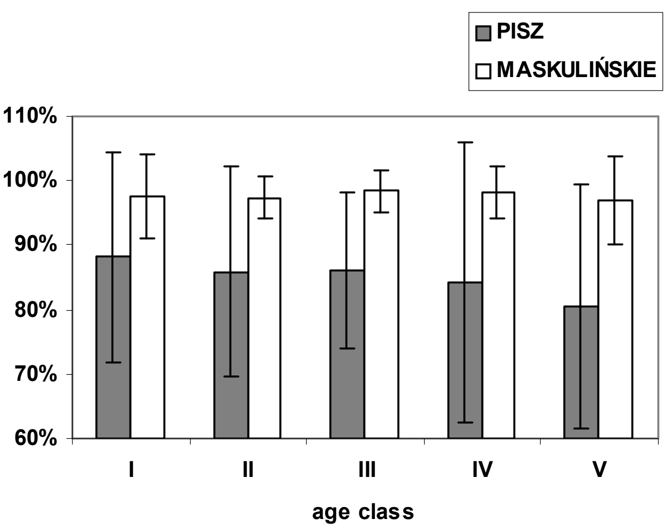

Fig. 3. Proportion of forest species individuals in carabid beetle assemblages inhabiting stands affected by the hurricane (P) and control stands (M) in age classes I-V.

Tab. 2. ANOVA for carabid beetle assemblages. Symbols used in pair-wise *post-hoc* tests: P – stands affected by the hurricane, M – control stands, I-V – age classes.

Variable	df	MS	F	*p*	LSD *post-hoc* test
Proportion of large zoophages					
site	1	1260.221	4.207	0.042	P > M (p = 0.042)
age	4	591.038	1.973	n.s.	-
site x age	4	1176.634	3.928	0.005	PI > PV, MI (p < 0.01-0.0001); PII, PIII, MIII > MI (p < 0.001); PIV, MII > MI (p < 0.001); PV < MIII (p < 0.050); MIV, MV > MI (p < 0.020)
Proportion of forest species					
site	1	6119.766	37.515	< 0.001	P < M (p < 0.001)
age	4	73.551	0.451	n.s.	-
site x age	4	50.797	0.311	n.s.	-
Proportion of European species					
site	1	15296.500	42.185	< 0.001	P < M (p < 0.001)
age	4	1182.071	3.260	0.014	II, IV < III (p < 0.005); V < III (p < 0.010)
site x age	4	382.986	1.056	n.s.	-
Proportion of autumn breeders					
site	1	12782.640	33.615	< 0.001	P < M (p < 0.001)
age	4	1100.858	2.895	< 0.001	II, IV, V < III (p < 0.010)
site x age	4	444.184	1.168	n.s.	-
Proportion of xerophilous species					
site	1	14643,71	38,01697	< 0,001	P > M (p < 0,001)
age	4	773,73	2,00869	n.s.	-
site x age	4	751,60	1,95125	n.s.	-
Proportion of hygrophilous species					
site	1	8905.812	72.867	< 0.001	P < M (p < 0.001)
age	4	369.404	3.022	0.020	I < IV (p < 0.005); I < V (p < 0.050); II < IV (p < 0.050)
site x age	4	106.732	0.873	n.s.	
SPC					
site	1	78102.740	36.014	< 0.001	P < M (p < 0.001)
age	4	7370.874	3.399	0.011	I < III (p < 0.050); II, IV < III (p < 0.010); V < III (p < 0.001)
site x age	4	1071.081	0.494	n.s.	-

MIB					
site	1	0.028	2.550114	n.s.	-
age	4	0.094	8.520429	< 0.001	I < III (p < 0.005); II < III (p < 0.010); IV, V < II (p < 0.050); IV, V < III (p < 0.001)
site x age	4	0.022	1.948175	n.s.	-

A contrasting trend was noticed for open habitat species. This environmental group seemed to be favoured by disturbance and increased considerably in abundance and richness in the disturbed stands (Tab. 1). Amongst all open habitat species the most pronounced changes refer to *Amara* and *Harpalus* spp (Tab. 1), which were markedly more numerous on site P (137 *Amara* individuals and 38 *Harpalus* individuals) than on site M (2 and 3 individuals respectively). Significant differences were also revealed for autumn breeders and European species. Both of these groups were negatively affected by the hurricane and considerably decreased in abundance in the disturbed stands (LSD test, $p < 0.001$ for both European and autumn breeding species) with the reduction in their proportion in the assemblages reaching 25% (Tab. 2). Windthrow contributed significantly (LSD test, $p < 0.001$) also to a 14-22% decline in the proportion of hygrophilous species (e.g. *Pterostichus niger*) individuals in assemblages (Fig. 4, Tab. 1, Tab. 2). Moreover it was found that the proportion of individuals belonging to the hygrophilous species in communities inhabiting young stands (age classes I, II) was considerably lower in comparison with that of old stands (age classes IV, V) (LSD test, p = 0.050-0.005, Tab. 2).

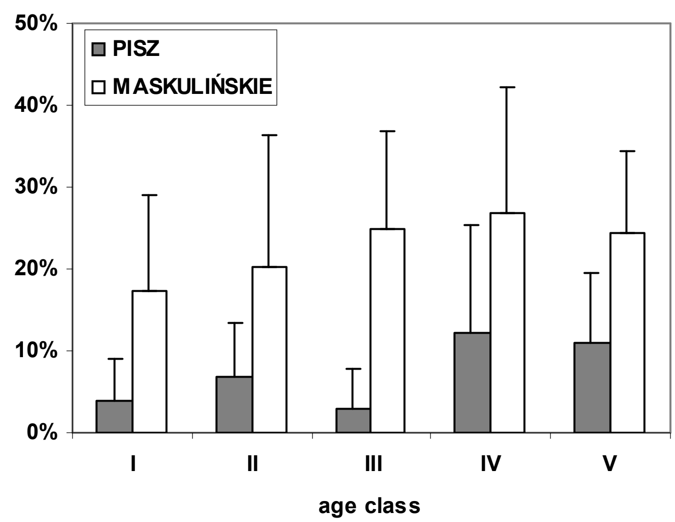

Fig. 4. Proportion of hygrophilous species individuals in carabid beetle assemblages inhabiting stands affected by the hurricane (P) and control stands (M) in age classes I-V.

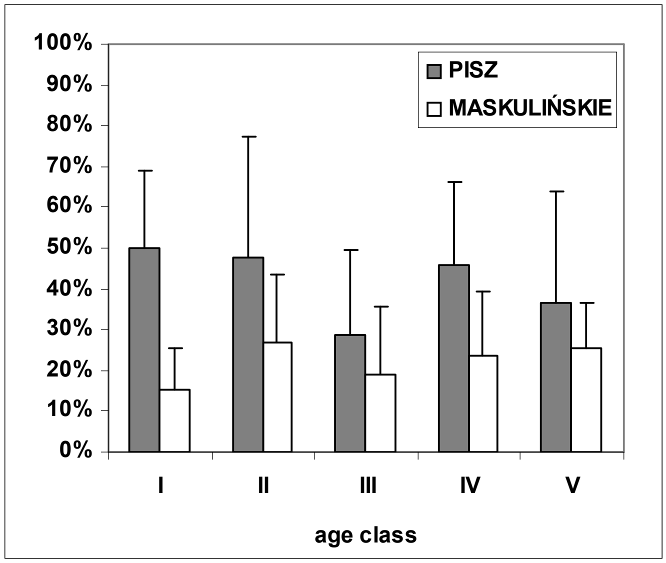

Fig. 5. Proportion of xerophilous species individuals in carabid beetle assemblages inhabiting stands affected by the hurricane (P) and control stands (M) in age classes I-V.

The opposite trend was observed for xerophilous species (e.g. *Amara lunicollis*). This group responded positively to disturbance (LSD test, $p < 0.001$) as their proportion in carabid assemblages increased by 10-35% in damaged P stands compared to the control M stands (Fig. 5, Tab. 2).

Interestingly, the proportion of large zoophages in carabid assemblages inhabiting stands affected

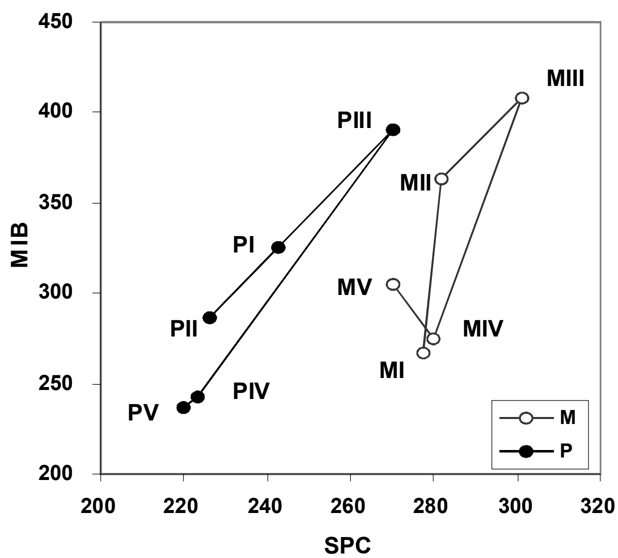

Fig. 6. The SPC/MIB (SCP/SBO) model of carabid beetle assemblages inhabiting stands affected by the hurricane (P) and control stands (M) in age classes I-V.

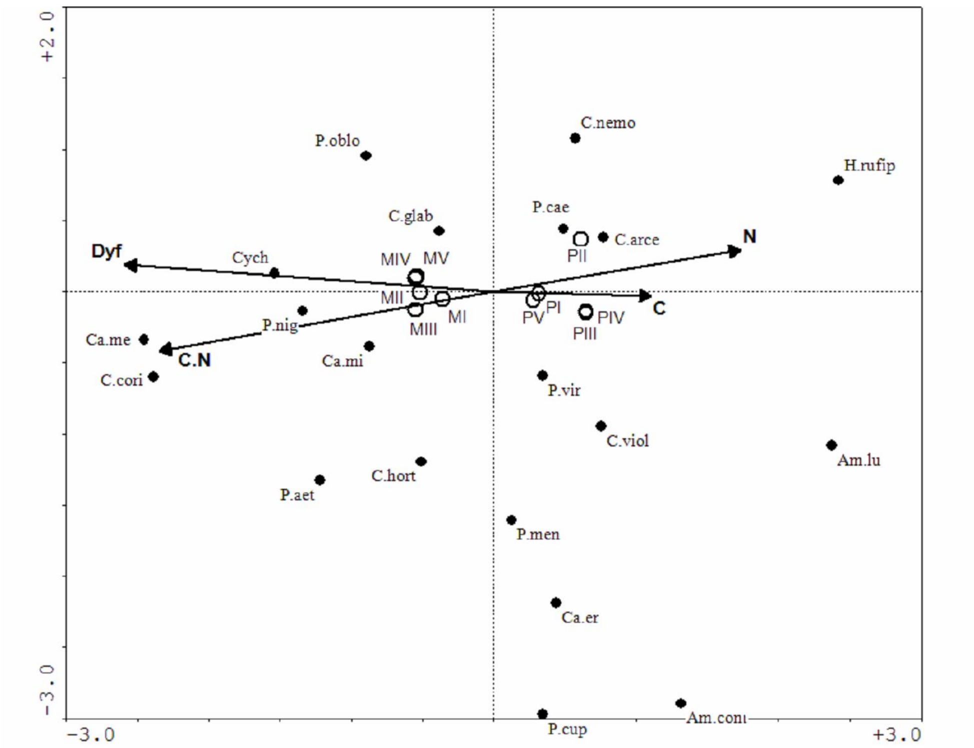

Fig. 7. CCA ordination of carabid beetle assemblages inhabiting stands affected by the hurricane (P) and control stands (M) in age classes I-V. Abbreviations of the environmental variables: N – nitrogen content of soil, C – carbon content of soil, C.N – C/N ratio of soil, Dyf – soil CO_2 efflux rate. (For full names of species, see Table 1).

by the hurricane was significantly higher than in the control stands (LSD test, $p < 0.05$), with the differences confirmed reaching 27% (Tab. 2). However, a large zoophage prevailing considerably in disturbed stands was *C. arcensis,* which was classified as a xerophilous species (Tab. 1). Moreover, it was accompanied by *P. caerulescens* (on PI site) and *A. lunicollis* (on PII, PIII, PIV and PV sites), which are included among non-forest species, whereas in the control stands, the most abundant large zoophage was *P. niger*, which is regarded as mesophilous-hygrophilous species (Tab. 1).

The differentiation of SPC and MIB values between disturbed and control sites are presented in the SPC/MIB model (Fig. 6). Although these differences do not seem to be pronounced, P stands are located [on the plot] on the left from M stands towards lower SPC/MIB values, which indicates changes in carabid assemblages brought about by the hurricane.

The 2-way ANOVA (Tab. 2) confirmed significant differences in carabid assemblages SPC values between stands of particular age classes ($F = 3.399$, $p < 0.05$), as well as between disturbed P and non-disturbed M sites ($F = 36.014$, $p < 0.001$). The SPC values recorded in stands affected by the hurricane were 11-25% (31-57 units) lower than in the control stands (LSD test, $p < 0.001$). Considering the stand age, the highest SPC values were recorded for carabid assemblages inhabiting stands of age class III (LSD test, p < 0.05-0.001).

Mean individual biomass (MIB) differed significantly between stands of particular age (F = 8.52, p < 0.001), with the highest values noted in stands of age class III (LSD test, p < 0.01-0,001). However, no significant differences in MIB between disturbed and non-affected stands were observed (Tab. 2).

Significant differences in carabid assemblage characteristics were also indicated by the canonical analysis. The CCA separated the carabid assemblages into disturbed stands (PI-PV) and control stands (MI-MV) groups with no overlap (Fig. 7). The horizontal axis was correlated with moisture gradient, as indicated the species distribution on diagram (Fig. 7). Disturbed stands PI-PV were located on the right from the vertical axis and control stands MI-MV formed a separate cluster on the left. The horizontal axis explained 82.1% of the total variation in the species and stands data [Monte Carlo permutation test: F = 4.678, p = 0.05]. Environmental variables that showed the strongest correlation with the horizontal axis were: C/N ratio of soil (r = - 0.80) and soil CO_2 efflux rate (r = - 0.89).

Discussion

Effect of hurricane on carabid assemblages species richness

Carabidae are regarded as sensitive indicators of changes occurring in the forest environment, including large-scale disturbances e.g. clear-cuts, windthrows and forest fires (Bouget 2005a; Skłodowski 1995a; Szyszko 1983, 1990, 2002). Carabid beetle responses to the disturbance in Pisz Forest District, reported by Skłodowski & Zdzioch (2005a, 2005b, 2006) from 2003 and 2004, were confirmed in the third year of the study as well. The hurricane significantly increased Carabidae assemblages' species richness, as in the damaged P stands considerably more species were recorded in comparison with the control M site (Tab. 1). Similar results from windthrow gaps have been so far reported by Bouget (2005), Bouget & Duelli (2004), Duelli & Orbist (1999) and Duelli *et al.* (2002). Moreover, an increase in carabid species richness in stands affected by a hurricane was positively correlated with gap size (Bouget 2005).

Other types of disturbances, as for example clear-cuts, may also lead to an increase in carabid species richness. Skłodowski (2002) reported that clear-cuts in pine stands were inhabited by a higher number of Carabidae species than adjacent uncut stands. According to Szyszko (1983), carabid catchability in pine stands declines with increasing stand age, as the highest carabid richness is observed in pine plantations. However, it must be pointed out that stands affected by a natural disturbance (e.g. hurricane or fire) and set aside without any human interference, differ significantly in terms of environmental variables from clear-cuts (Bengtsson *et al*. 2000; Niemelä 1999; Similä *et al*. 2002; Skłodowski & Zdzioch 2006). In clear-cut areas, most of the dead wood, especially that of large diameter, is removed after logging and the soil is usually subjected to preparation (i.e. ploughing in rows), which destroys litter and moss-cover (Sippola *et al.* 1998; Skłodowski & Zdzioch 2005a). A hurricane, according to a literature review made by Ulanova (2000), not only causes more pronounced damage to middle-aged and mature stands but also increases environmental heterogeneity. Contrary to clear-cuts, windthrow gaps are not homogenous areas, as the hurricane creates a complex mosaic of diverse microhabitats comprising coarse woody debris of different types and diameter, e.g. stumps, snags, fallen logs and branches and leaning or uprooted trees, as well as root plates, pits and mounds caused by their collapse (Bobiec 2002; Bouget 2005a; Faliński, 1986; Sippola *et al.*, 1998; Skłodowski and Zdzioch 2006; Ulanova 2000). Moreover, canopy openings stimulate the development of a herb layer (Bouget 2005a). Each of these microhabitats may be used by certain carabid species of different ecological and trophic groups, such as foraging, sheltering or overwintering sites (Bouget 2005a; Bouget & Duelli 2004; Niemelä & Halme 1992; Skłodowski & Zdzioch 2006), and they may also support the re-colonization of gaps by Carabidae (Skłodowski, 2002). Apparently the windthrow gaps˙ heterogeneity contributed to higher overall carabid species richness in disturbed stands compared to control areas, however it also resulted in uneven distribution of particular carabid species within the canopy openings and in consequence – along the trapping plots. Each of the microhabitats created by the hurricane within the gaps could host different set of species with specific preferences towards soil moisture, sun exposure, litter depth etc. Thus each of the microhabitat patches supported only some of the species recorded from the whole stand. Therefore the mean number of species caught per trap in disturbed stands was lower in comparison with the more homogenous control stands, where particular carabid species were distributed more evenly along the trapping plots.

Certain forest species were still recorded in disturbed P stands, e.g. *Carabus arcensis, C. violaceus, Pterostichus niger, P. oblongopunctatus* (Tab. 1), which is consistent with the observations of Otte (1989) and Bouget (2005a). One of the crucial factors influencing carabid beetle presence is the litter layer (Niemelä & Halme 1992; Skłodowski & Zdzioch 2006). Contrary to clear-cuts, where the top-soil is usually ploughed in rows, in windthrow gaps the soil profile remains mainly undisturbed (however, some pits and mounds are created by uprooted trees) and the litter layer and moss cover are still present (Skłodowski & Zdzioch 2006). The importance of forest litter for carabid beetles has already been discussed by many authors. It may serve as a foraging area or a shelter from predators, as well as from unfavourable weather conditions (e.g. drought and frost). Thus the presence of deep leaf litter favours the occurrence of many Carabidae species, especially those associated with forest and shade, however the open habitat species may show an inverse trend (Koivula 2001; Koivula *et al.* 1999; Pihlaja *et al.* 2006; Skłodowski 2002).

Also the "forest islands" in windthrow gaps, consisting of groups of trees that survived the hurricane, could apparently act as refuges for forest species, enabling them to re-colonize the open area (Skłodowski 2002; Skłodowski & Zdzioch 2006). Moreover, the presence of forest species in stands affected by the hurricane could also be ascribed to their dispersal from adjacent forest stands (Grechanichenko & Guseva 2000; Skłodowski 2002).

On the other hand, canopy openness contributed significantly to increase in sunlight, moss cover degeneration and desiccation of the soil and litter layers (Sławski 2007; Skłodowski & Buszyniewicz, 2007), which apparently lead to the influx of xerophilous carabids, comprising *Amara* and *Harpalus* species (Tab. 1). Moreover, many specialists associated with the initial successional stages, that are able to efficiently colonize open habitats, also seem to be favoured by windthrow. Together with web-weaving and epigeic spiders, in disturbed ecosystems the latter are noted to be prevalent (Bouget & Duelli 2004). In windthrow gaps, many ubiquitous species may also be abundant, as has been observed in small clear-cut areas (Koivula 2001; Koivula *et al.* 2002; Skłodowski & Zdzioch 2006). Apparently all the above mentioned factors contribute to the significant increase in overall Carabidae species richness in stands disturbed by the hurricane, in comparison with control stands.

Carabid abundance in windthrows

Windthrow considerably decreased Carabid abundance, which is consistent with results obtained by Bouget (2005a) for windthrow gaps. The total number of Carabidae specimens, as well as the mean number of individuals caught per trap in P stands, was significantly lower than in control M areas (Tab. 1). The occurrence of carabid beetles depends not only on the presence of litter layer (e.g. *Carabus glabratus*) and habitat heterogeneity but it is also conditioned by the availability of potential prey (Niemelä & Halme 1992). The low Carabidae abundance recorded in disturbed stands was probably caused both by the low biological activity of the soil, and by low abundance of litter arthropods i.e. potential prey for carabids (Harrison 1987). According to many authors (e.g. Bouget & Duelli

2004; Skłodowski 2007; Sławska & Sławski 2007; Tracz 2007), increased temperature variability as well as litter and soil desiccation brought about by increased exposure to sunlight and wind in canopy gaps, reduces both soil and litter microorganism's activity, as well as abundance of litter arthropods. Decomposers, such as *Diplopoda*, *Isopoda* and both hemiedaphic and eudaphic *Collembola,* are among the litter arthropods that suffer the most from litter desiccation, however the atmobiontic *Collembola* may increase in numbers. The decline in overall litter arthropod abundance might therefore contribute to the reduction in abundance of some carabid zoophage species that feed on them. The soil CO_2 efflux rate, as the measurement of its biological activity, was 20-30% lower in disturbed P stands, compared to the control M stands (Skłodowski 2007). The decrease in soil CO_2 efflux rate observed in windthrow gaps was accompanied by a reduction in the C/N ratio of the soil. Usually the decline in C/N ratio results from high organic matter decomposition rate and high biological activity of soil. However, together with low soil CO_2 efflux rate, the decrease in C/N ratio apparently could be ascribed to reduced biological activity of soil, as soil and litter *Collembola*, microorganisms and fungi, particularly those connected with nitrogen immobilization, are negatively affected by soil desiccation, which results in poor nitrogen immobilization and nitrogen accumulation in the soil (Skłodowski 2007). The CCA ordination indicated that both soil CO_2 efflux rate and C/N ratio of soil were positively correlated with data obtained for carabid assemblages inhabiting control stands, whereas in the case of carabid assemblages from stands affected by the hurricane, a negative correlation was observed (Fig. 7).

Effect of hurricane on carabid assemblages structure

Changes in microclimatic conditions and soil humidity, caused by windthrow, contributed significantly not only to carabid abundance but also to their structure and composition. Both the Ward's cluster analysis and CCA canonical analysis clearly divided carabid assemblages into groups of disturbed and non-affected stands, without overlap (Fig. 1, Fig. 7). Moreover, the CCA analysis indicated that the main factor explaining most of the variation between these groups was habitat moisture.

Generally, habitat conditions following disturbance apparently favour different species assemblages from those of non-disturbed ecosystems. Considering windthrows, the most usual fauna comprise xerophilous and open-land species, as well as specialists colonizing forest ecosystems in the initial stages of succession. Eurytopic species that are tolerant to habitat changes are also observed significantly more frequently (Bouget 2005a). On the other hand, disturbance contributes considerably to a decline in species richness and increased abundance of stenotopic forest species, which are unable to thrive in damaged stands (Bouget 2005a). Corresponding changes in carabid assemblages, i.e. significant decrease in the proportion of forest, European and autumn-breeding species, were observed in P stands affected by the hurricane (Tab. 2, Fig. 3). Similar results have been reported by many authors, e.g. in windthrow gaps (Bouget 2005a), in small clear-cuts (Koivula 2001; Koivula *et al.* 2002; Pihlaja *et al.* 2006; Skłodowski 2002) as well as in plantations and young forest stands set on clear-cuts (Skłodowski 1995a, 2006; Szyszko 1983).

As the proportion of forest, European and autumn breeding species (combined with the proportion of large zoophages) contribute to the SPC index, the decline in these three groups' abundance led to a reduction in SPC values in disturbed P stands compared to the control M stands (Tab. 2, Fig. 6). This result is consistent with the observation of Skłodowski (2006), as SPC indicates the successional stage of the carabid assemblages, in disturbed stands a significant reduction in SPC is recorded.

Moreover, the desiccation of soil and litter in windthrow gaps contributed significantly to an increase in the proportion of xerophilous species comprising *Amara* and *Harpalus* individuals, at the expense of hygrophilous species (Tab.

1, Tab. 2, Fig. 4, Fig. 5). The carabid assemblages of non-disturbed M stands were dominated by *P. niger*, a mesophilous species which prefers moist litter and avoids desiccated microhabitats, whereas assemblages of disturbed P stands were characterized by the extremely high (almost 50%) predominance of the xerophilous species *C. arcensis* (Tab. 1).

Interestingly the proportion of large zoophages in the assemblages of disturbed stands was slightly higher than in control stands (Tab. 2). Moreover, no significant differences in MIB between these two stands types were demonstrated by the 2-way ANOVA analysis (Tab. 2) whereas, according to the literature, as the ecosystem regeneration proceeds, the MIB value should increase significantly (Skłodowski 1995b; Szyszko 1983). Skłodowski (1995b) reported that in young pine stands, the MIB value may increase even twice in a period of 3-4 years.

Apparently the relatively high MIB values observed in the disturbed P stands were due to extremely high dominance of the large zoophage, *C. arcensis* (46,3% – Tab. 1). Despite being regarded as a forest species, *C. arcensis* seemed to favour a dry microclimate of windthrow gaps and was able to efficiently colonize them. It is consistent with the results obtained by Skłodowski (2001b, 2002), who observed that the catchability of *C. arcensis* was higher on small clear-cut areas compared to adjacent stands, as this carabid beetle had colonized the clear-cut easily and almost immediately after clearance, and was able to persist and breed there. In general, *C. arcensis* is an ecotone species inhabiting forest edges. Being a xerophilous species, *C. arcensis* is profoundly supported by canopy openings (e.g. windthrow gaps, clear-cuts), where increased sunlight exposure results in soil and litter layer desiccation (Skłodowski, 2001b, 2002). However not all the forest carabid species may successfully persist in forest gaps. Forest carabids requiring shade, moist or medium-moist habitat with a well developed litter layer and moss cover, e.g. *Carabus coriaceus, C. glabratus* and *C. violaceus* (Turin *et al.*, 2003), decline in abundance with increasing moss cover degeneration and soil desiccation and are not able to survive in canopy openings nor in small woodland islands (Matveinen-Huju *et al.* 2006; Skłodowski 2006). Thus the forest species *C. coriaceus*, that was numerously observed in control M site, was absent from disturbed stands (Tab. 1).

Conclusions

Changes observed in carabid assemblages on sites affected by a hurricane are profound, though similar to those recorded in many communities inhabiting disturbed ecosystems. A post-disturbance succession is characterized by an influx of species that are favoured by new, modified environmental conditions. Considering windthrown stands, a new carabid fauna was represented particularly by open habitat and xerophilous species that are well adapted to progressive desiccation of soil and litter surface. Their appearance resulted in a temporary increase in species richness (Skłodowski & Zdzioch, 2005a, 2005b, 2006), which was especially pronounced in the first year following the hurricane, as the forest fauna still persisted then. However, with the successional progress, a gradual disappearance of species unable to persist in post-disturbance ecosystem takes place. As the reduction of: soil humidity, CO_2 efflux rate and the C/N ratio proceeded, a significant decrease in the proportion of forest, European and autumn-breeding species in the carabid assemblages was observed, contributing furthermore to a significant reduction in SPC values. A forest stenotopic species, *C. coriaceus,* disappeared within a year following the hurricane, while some other forest and/or hygrophilous carabids might do so with a time delay. An interesting trend was observed for large zoophages. Contrary to years 2003 and 2004, in the third year following the hurricane, the proportion of these species in assemblages inhabiting disturbed stands was higher than in control stands (Skłodowski & Zdzioch 2005a, 2005b, 2006). It might be therefore concluded, that large zoophages typical of humid microhabitats and/or close forest are being replaced by large xerophilous zoophages with an affinity for colonizing windthrow gaps (*C. arcensis*), which is also consistent with the fact that differences in MIB values between disturbed and control sited were not significant.

Apparently the hurricane disturbance, modifying the ecosystem conditions and increasing heterogeneity, induced a series of successional changes in the carabid community, contributing to higher species richness and diversity. Forest assemblage replacement with assemblages typical of xerophilous and open habitat ecosystems takes place, however some forest and meso-higrophilous species still persist in gaps in more favourable microhabitats. It is now interesting, whether in the next year this succession will proceed towards a more open habitat and xerophilous community, or will the vigorous birch and pine regeneration in windthrow gaps rather switch it towards community characteristics of young forest stands.

Acknowledgements

The authors would like to thank Stephen Venn for his valuable comments and linguistic revisions of the text, which have greatly improved the previous version of the manuscript.

The authors would also like to thank to the Ministry of Science and Higher Education (project number 2PO6L02626) for financial support.

References

Bengtsson J., Nilsson S.G., Franc A., Menozzi P. 2000. Biodiversity, disturbances, ecosystem function and management of European forests. For. Ecol. Manage. 132: 39–50.

Bobiec A. 2002. Living stands and dead wood in the Białowieża forest: suggestions for restoration management. For. Ecol. Manage. 165: 125–140.

Bouget C. 2005a. Short-term effect of windthrow disturbance on ground beetle communities: gap and gap size effects. European Carabidology 2003. Proceedings of the 11th European Carabidologist Meeting. DIAS Report. No 114: 25–39.

Bouget C. 2005b. Short-term effect of windstorm disturbance on saproxylic beetles in broadleaved temperate forests. Part II. Effects of gap size and gap isolation. For. Ecol. Manage. 216: 15–27.

Bouget C., Duelli P. 2004. The effect of windthrow on forest insect communities: a literature review. Biological Conservation 118: 281–299.

Burakowski B., Mroczkowski M., Stefanska J. 1973-1974. Katalog Fauny Polski, Chrząszcze Coleoptera, Biegaczowate, Carabidae, Vol. XXIII, t. 3-4. PWN. [In Polish.]

Chapin F.S. III, Matson P.A., Mooney H.A. 2002. Principles of terrestrial ecosystem ecology. Springer-Verlag New York, Inc. pp. 435.

Duelli P., Orbist M.K. 1999. Räumen oder belasen? Die Entwicklung der faunistichen Biodiversität auf Windwurfflächen im Schweizerichen Alpenraum. Versh. Ges. Oekol. 29: 193–200.

Duelli P., Orbist M.K., Wermelinger B. 2002. Windthrow included changes in faunistic biodiversity in alpine spruce forests. For. Snow Landsc. Res 77, 1,2: 117–131.

Faliński J.B. 1986. Vegetation dynamics in temperate lowland primeval forest. Ecological studies in Białowieża Forest. W. Junk. Dordrecht. pp. 537.

Grechanichenko T., Guseva N. 2000. Carabid communities (Col. Carabidae) in different forest biotopes in central forest steppe. Entomol. Rev. 80: 592–599.

Harrison S. 1987. Tree fall gaps versus forest understory as environments for a defoliating moth on a tropical scrub. Oecologia 72: 65–68.

Ings T.C., Hartley S.E. 1999. The effect of habitat structure on carabid communities during the regeneration of a native Scottish forest. For. Ecol. Manage. 119: 123–136.

Kaila L., Martikainen P., Punttila P. 1997. Dead trees left in clear-cuts benefit saproxylic Coleoptera adapted to natural disturbances in boreal forest. Biodiv. Conserv. 6: 1–18.

Koivula M. 2001. Carabid beetles (Coleoptera, Carabidae) in boreal managed forests – meso-scale ecological patterns in relation to the modern forestry – PhD thesis, University of Helsinki. pp. 120.

Koivula M., Kukkonen J., Niemelä J. 2002. Boreal carabid beetle (Coleoptera, Carabidae) assemblages along the clear-cut originated succession gradient. Biodivers. Conserv. 11: 1269–1288.

Koivula M., Punttila P., Haila Y,. Niemelä J. 1999. Leaf litter and the small-scale distribution of carabid beetles (Coleoptera, Carabidae) in the boreal forest. Ecography 22: 424–435.

Krebs C. J. 1999. Ecological methodology. Second edition. Addison Wesley Longman pp. 620.

Larsson S.G. 1939. Entwicklungstypen und Entvicklungszeiten der Dänishen Carabiden. Entomologiske Meddelelser 20: 273–562.

Linder P., Östlund L. 1998. Structural changes in three mid-boreal Swedish forest landscapes, 1885-1996. Biol. Conserv. 85: 9–19.

Lindhe A., Åsenblad N., Toresson H.-G. 2004. Cut logs and high stumps of spruce, birch, aspen and oak – nine years of saproxylic fungi succession. Biol. Conserv. 119: 443–454.

Lindhe A., Lindelöw Å. 2004. Cut high stumps of spruce, birch, aspen and oak as breeding substrates for saproxylic beetles. For. Ecol. Manage. 203: 1–20.

Matveinen-Huju K., Niemelä J., Rita H., O˙Hara R. 2006. Retention-tree groups in clear-cuts: Do they constitute 'life-boats for spiders and carabids? For. Ecol. Manage. 230: 119–135.

Niemelä J. 1999. Management in relation to disturbance in the boreal forest. For. Ecol. Manage. 115: 127–134.

Niemelä J., Halme E. 1992. Habitat associations of carabid beetles in fields and forests on the Aland Islands, SW Finland. Ecography 15: 3–11.

Otte J. 1989. Ecological investigations on the importance of wind-throw areas for the insect fauna. Part II. Waldhygiene 18: 1–36.

Pascarella J.B., Aide T.M., Zimmerman J.K. 2004. Short-term response of secondary forests to hurricane disturbance in Puerto Rico, USA. For. Ecol. Manage. 199: 379–393.

Pickett S.T.A., White P.S. 1985. The ecology of natural disturbance as patch dynamics. Academic Press, New York.

Pickett S.T.A., Wu J., Cadenasso M.L. 1999. Patch dynamics and the ecology of disturbed ground: a framework for synthesis - In: Walker, L.R. [ed.] Ecosystems of disturbed ground. Elsevier, Amsterdam. 707–722.

Pihlaja M., Koivula M., Niemelä J. 2006. Responses of boreal carabid beetle assemblages (Coleoptera, Carabidae) to clear-cutting and top-soil preparation. For. Ecol. Manage. 222: 182–190.

Pontailler J.-Y., Faille A., Lemée G. 1997. Storms drive successional dynamics in natural forests: a case study in Fontainebleau forest (France). For. Ecol. Manage. 98: 1–15.

Poole A., Gormally M., Skeffington M.S. 2003. The flora and beetle fauna of a mature and regenerating semi-natural oak woodland in south-east Ireland. For. Ecol. Manage. 177: 207–220.

Similä M., Kouki J,. Martikainen P., Uotila A. 2002. Conservation of beetles in boreal pine forests: the effects of forest age and naturalness on species assemblages. Biol. Conserv. 106: 19–27.

Sippola A.L., Siitonen J., Kallio R. 1998. Amount and quality of coarse woody debris in natural and managed coniferous forests near the timberline in Finnish Lapland. Scand. J. For. Res. 13: 204–214.

Sławska M., Sławski M. 2007. The dynamics of composition and structure of epigeic-soil communities of Collembola in the stands of Pisz Forests destroyed by the hurricane. – In: Skłodowski J. (ed.), Zooindicative monitoring of hurricane caused damage of forest ecosystems of Pisz Forest: 53–95. Warsaw Agricultural University Press. [In Polish with English summary.]

Sławski M. 2007. Dynamics of forest floor vegetation in the wind destroyed plots of Pisz Forest District. – In: Skłodowski J. (ed.), Zooindicative monitoring of hurricane caused damage of forest ecosystems of Pisz Forest: 35–46. Warsaw Agricultural University Press. [In Polish with English summary.]

Skłodowski J. 1995a. Antropogeniczne przeobrażenia zespołów biegaczowatych (Col. Carabidae) w ekosystemach borów sosnowych Polski. [Anthropogenic changes in carabid assemblages (Col. Carabidae) in pine forest ecosystems in Poland.] – In: Szujecki A. *et al*. (eds.), Antropogeniczne przeobrażenia epigeicznej i glebowej entomofauny borów sosnowych Polski: 17–174. Katedra Ochrony Lasu i Ekologii, Fundacja „Rozwój SGGW", Warszawa. [In Polish.]

Skłodowski J. 1995b. Soil fertilization and acidification effect on the rate of dvelopment of epigeic carabid (Coleoptera, Carabidae) communities in a Scots Pine forest plantation. Folia forestalia Polonica A – Forestry, 37: 21–46.

Skłodowski J. 1997. Interpretacja stanu środowiska leśnego za pomocą modelu SCP/SBO zgrupowan biegaczowatych (Col. Carabidae). Interpretation of state of environment by using SPC/MIB model of carabid assemblages. – In: Mazur, S. *et al*. (eds.), Waloryzacja ekosystemów lesnych metodami zooindykacyjnymi. VI Sympozjum Ochrony Ekosystemów Lesnych. Jedlnia 2-3 grudnia 1996: 69–87. Fundacja Rozwój SGGW. [in Polish.]

Skłodowski J. 2001a. Waloryzacja siedlisk leśnych Puszczy Białowieskiej na podstawie *Carabidae*. [Valorization of forest stands in Białowieska Primeval Forest using carabid beetles] – In: Szujecki A. et al. (eds.), Próba szacunkowej waloryzacji lasów Puszczy Białowieskiej metodą zooindykacyjną: 73–104. Wydawnictwo SGGW, Warsaw Agricultural University Press. pp. 411. [In Polish.]

Skłodowski J. 2001b. The structure of Carabid communities in some Fidel-forest ecotones. Balic J. Coleopterol. 1 (1–2): 41–52.

Skłodowski J. 2002. System kolonizacji zrębu zupełnego przez biegaczowate oraz możliwości jego doskonalenia. Rozprawa habilitacyjna. [System of colonization clear-cut area by carabid beetles and possibility of its improving.] Wydawnictwo SGGW, Warsaw Agricultural University Press.pp. 134. [In Polish with English summary.]

Skłodowski J. 2006. Anthropogenic transformation of ground beetle assemblages (Coleoptera: Carabidae) in Białowieża Primeval Forest, Poland: from primeval forests to managed woodlands of various ages. Entomol. Fennica 17: 296–314.

Skłodowski J. 2007. Selected indices describing the status of the environment. In: Skłodowski J. (ed.), Zooindicative monitoring of hurricane caused damage of forest ecosystems of Pisz Forest: 21–34. Warsaw Agricultural University Press. [In Polish with English summary.]

Skłodowski J., Buszyniewicz J. 2007. Forest floor dynamics in the stands destroyed by the hurricane results of the onground photographic recording method. In: Skłodowski J. (ed.), Zooindicative monitoring of hurricane caused damage of forest ecosystems of Pisz Forest: 47–51. Warsaw Agricultural University Press. [In Polish with English summary.]

Skłodowski J., Zdzioch P. 2005a. Biegaczowate (Carabidae, Col.) drzewostanów Puszczy Piskiej zniszczonej przez huragan – rok „zero". Sylwan 5: 43–51.

Skłodowski J., Zdzioch P. 2005b. "The day after" – first year of carabid recolonization of pine forest damaged by hurricane. In J. Skłodowski *et al*. Protection of Coleoptera in The Baltic Sea Region. p. 185–193.

Skłodowski J., Zdzioch P. 2006. Ground beetles (Coleoptera: Carabidae) in second year of regenerative succession of Pisz forests destroyed by hurricane. Wiad. Entomol. 25, Supl. 1: 97–110. [In Polish with English summary].

StatSoft Inc. 1997. Statistica for Windows (Computer program manual). - Tulsa, OK, USA.

Szujecki A., Mazur S., Perliński S., Szyszko J. 1983. The process of forest soil macrofauna formation after afforestation of farmland. Warsaw Agricultural University Press, Warsaw 1983.

Szyszko J. 1983. State of Carabidae (Col.) fauna in fresh pine forest and tentative valorisation of this environment. – Warsaw Agricultural University Press.

Szyszko J. 1990. Planning of prophylaxis in threatened pine forest biocenoses based on an analysis of the fauna of epigeic Carabidae. - Warsaw Agricultural University Press.

Szyszko J. 2002. Carabids as an efficient indicator of the quality and functioning of forest ecosystems useful in forest management. In: Szyszko, J. *et al.* (eds.), How to protect or What we know about Carabid Beetles. From knowledge to application – from Wijster (1969) to Tuczno (2001): 301–318. Warsaw Agricultural University Press. pp. 378.

Tracz H. 2007. Diplopoda and Chilopoda fauna in the ecosystems of posthurricane and control stands. In: Skłodowski J. (ed.), Zooindicative monitoring of hurricane caused damage of forest ecosystems of Pisz Forest: 97–105. Warsaw Agricultural University Press. [In Polish with English summary.]

ter Braak C.J.F, Smilauer P. 1997. Canoco for Windows – Version 4.02. [Computer program manual]. Centre for Biometry. Wageningen. The Netherlands.

Turin H. 2000. De Nedrelandse loopkevers. Verspreiding en oecologie (Coleoptera: Carabidae). Nationaal Natuurhistirisch Museum Naturalis. – KNNV Uitgeverij. pp. 662. [In Dutch.]

Turin H., Pener L., Casala A. 2003. The Genus Carabus in Europe. A Synthesis. Fauna Europaea Evertebrata No. 2, Sofia– Moscow.

Ulanova N.G. 2000. The effects of windthrow on forests at different spatial scales: a review. Forest Ecology and Management 135: 155–167.

Wolf A., Møller P.F., Bradshaw R.H.W., Bigler J. 2004. Storm damage and long-term mortality in a semi-natural, temperate deciduous forest. For. Ecol. Manage. 188: 197–210.

Zackrisson O. 1977. Influence of forest fires on the north Swedish boreal forest. Oikos 29: 22–32.

Received: 12.01.2007.
Accepted: 31.05.2007.