CHANGES OF SECONDARY PRODUCTIVITY OF CARABID COMMUNITIES (INSECTA: COLEOPTERA) IN NATURAL FOREST ECOSYSTEMS IN RELATION TO GEOLOGICAL SUBSTRATE AND VERTICAL ZONALITY

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Abstract. *The secondary productivity of 48 carabid communities from natural forests on different geologic substrates and at different altitudes is compared. In spite of a great variability, it shows a decreasing trend from communities form habitats on alkaline or nitrophilous substrates to the acidic substrates and from low altitudes to the high altitudes. In communities on more fertile substrates, a considerable part of biomass is bound by large species occurring in a lower number of individuals, whereas on the less fertile substrates the existing biomass tends to be split among a large number of little species. In some cases, the direct influence of the habitat trophicity or climatic factors is combined with indirect influence of litter structure or its continuous covering by mosses.*

Keywords: *Carabidae, secondary productivity, geological substrate, vertical zonality.*

Rezumat. Schimbările productivităţii secundare ale cenozelor de carabide (Insecta: Coleoptera) din ecosisteme forestiere naturale în relaţie cu substratul geologic şi zonalitatea verticală. *Compararea productivităţi secundare a 48 de cenoze de carabide din păduri naturale de pe substrat geologic şi altitudine diferită a arătat că, în ciuda variabilităţii mari, există un trend descrescător de la cenozele din biotopii de pe substratele alcaline sau nitrofile până la cele acidofile, precum şi din altitudinele mici până la cele înalte. În cenozele de pe substrate mai bogate, o mare parte a biomasei este legată de specii mari care se întâlnesc în număr relativ mic. Spre deosebire, pe substratele mai sărace, biomasa tinde să fie împărţită între un număr mare de specii mici. În unele cazuri, influenţa directă a substratului sau a factorilor climatici este combinată cu influenţă indirectă a structurii de litieră sau acoperirea ei continuă de muşchi.*

Cuvinte cheie: *carabide, productivitate secundară, substrat geologic, zonalitate verticală.*

INTRODUCTION

Geological substrate and vertical zonality of climate belong to the most important abiotic factors responsible of productivity of ecosystems. The geological substrate indirectly influences the hydrological regime in ecosystems and directly influences the soil fertility, which increases from the acid soils to the nitrophilous or alkaline soils. The production of plant communities determines the food basis for herbivores and, secondarily, of carnivores and destructors. The aim of this contribution is to show, how the productivity of carabids communities changes along the geologic and climatic gradients in the natural forest stands in Central Europe.

MATERIAL AND METHODS

The material was pitfall trapped in 48 habitats in 16 localities (ŠUSTEK 1972, 1976, 1982, 1983, 1984, 1986, 1988, 2006, Tab. 1) in Bohemia, Moravia and Slovakia in 1970-2006: Malá Pleš 49°59'4"N, 13°49'32"E; Kohoutov 49°59'43"N, 13°50'29"E; Hřebínek 50°50'54"N, 15°16'2"E; Žákova hora 49°41'1"N, 16°1'15"E; Františkova Myslivna 50°3'27"N, 17°12'28"E; Pavlovské kopce 48°52'40"N, 16°39'33"E; Boleradice 48°58'23"N, 16°47'39"E; Buchlovice 49°5'57"N, 17°17'50"E; Kľačianska Magura 49°9'14"N, 18°57'40"E; Šrámková 49°11'13"N, 19°7'11"E; Zadná Javorová dolina 49°12´40"12N, 20°9'19"E., Kolová dolina 49°10'14"N, 20°10'30"E, Zadné Meďodoly 49°14'10"N, 20°10'44"E. More detailed characteristics of the localities are given in the papers cited above. In these papers the complete surveys of species are also given.

The ecological conditions in these habitats are characterized according to the Zlatník´s system of phytocoenological classification of natural forests in the Central Europe (ZLATNÍK & RAUŠER 1966, ZLATNÍK 1976), which in relation to the geological substrate distinguishes four trophic series (A-acidophilous, B-neutral, C-nitrophilous, D-alkaline) and three transition series (AB, BC and BD), while in rapport to sequence of altitudinal and expositional changes of climate defines nine vegetation tiers named according to dominant edificatory trees (oak, beech-oak, oak-beech, beech, beech-fire, beech-fire-spruce, spruce, dwarf pine, alpine meadows).

The habitats belonging purely to the alkaline trophic series D were omitted in this study, because the available material originates from the steppe-like formations with an extremely low occurrence of carabids. Also the floodplain ecosystems were intentionally omitted in this study, because the possible direct influence of the geologic substrate is here masked by a rich input of sediments, converging to the conditions in the nitrophilous series C. At the same time, the secondary production of Carabids in them is strongly subjected to natural fluctuations of hydrological regime and its profound anthropogenic changes.

The number of traps (glass or plastic jars with diameter of 75 mm, filled with 4% formalin) installed in each habitat varied according to purposes in the respective investigations. In the earlier studies (ŠUSTEK 1972, 1976, 1983), 10 traps were installed in homogenous habitats in accordance with the experimental study of OBRTEL (1971), while in the later studies (ŠUSTEK 2006) it was reduced to 6, as it has been shown that the suggested number of 10 traps is exaggerated (BLAŽEK & PAVLÍČEK 1986, ŠUSTEK, 1994). In the heterogeneous habitats (ŠUSTEK 1982, 1983, 1984; ŠUSTEK & ŽUFFA 1986, 1988), the trap number was adopted according to ecological gradients studied. In this case, the homogenous segments of transects were selected.

The cumulative biomass was calculated by multiplying the number of individuals standardized per one trap and one vegetation period by average dry weight of species. It was established by weighting at last 20 individuals after desiccation in a thermo stat at temperature 80°C for 24 hours, with accuracy on four decimal digits. In the rare species, like *Licinus hoffmannsegi*, only the available specimens were weighted (Table 2). This approach was adapted as a relatively simple way, evicting weighting of each specimen in the samples and, to certain degree, eliminating the individual differences in size and weight. The total weight of the one-year catch of carabids, calculated in the above way, is taken as measure of productivity of their communities.

The nomenclature of Carabids is adopted according to JELÍNEK (1993). In this study, 97 species are taken in consideration. Most of them are mesohygrophilous stenotopic forests species, characteristic of the respective types of natural forest. A minor part is represented by euryecious species or heliophilous species of open landscape, which penetrate the forests due to their fragmentation, especially in the lowlands.

RESULTS AND DISCUSSIONS

The Central European carabids show large differences in size of individual species, which reach from 1.6 mm (*Elaphropus parvulus* DEJEAN, 1831) to 40 mm (*Carabus coriaceus*). Hence the largest species is 25 times longer than the smallest species. These differences are still enhanced in the body weight: about 6.5 g in the largest *Carabus coriaceus* while about 0.001 g in the smallest species. Thus the largest species may be 6,500 times heavier than the smallest species (Table 2, Figs. 1 and 2).

Distribution of body weight among the species examined is very unequal. *Carabus coriaceus* with its 6.5 g takes a clearly isolated position, being followed by 8 species approximating a weight of 2 g, 10 species approximating a weight of 1.5 g and 6 species weighting about 0.5-1.0 g. The weight of the next 72 species decreases almost linearly, from a value of about 0.5 g to 0.004 g, but even in this species group an indication of a step-like decreasing pattern is visible. However, differences between these steps are minute (Fig. 2) and lay within the possible individual variability. The weight differences shown in Figs. 1 and 2, especially between the large species, and differences in occurrence of these species in individual habitats may essentially influence cumulative productivity of the respective communities, as shown bellow.

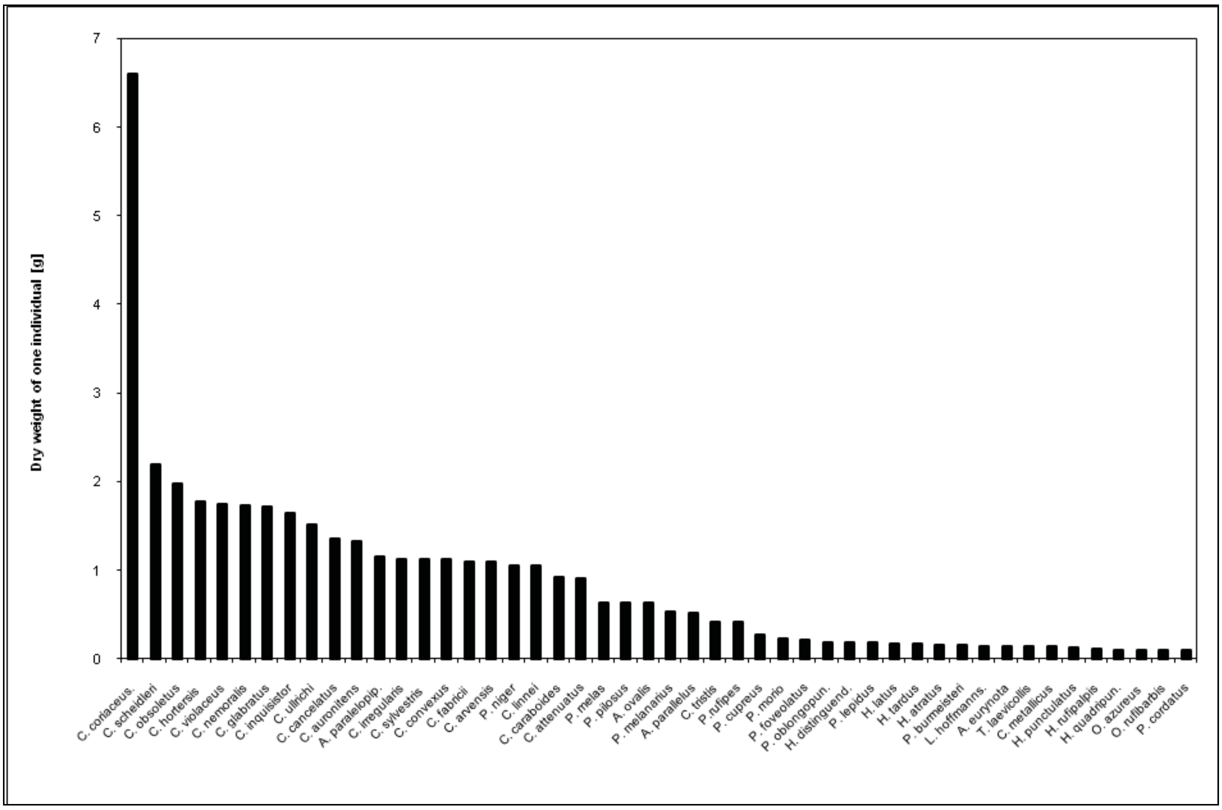

Figure 1. Average weight of Carabids species with the weight above 0.1 g.
Figura 1. Greutatea medie a speciilor de carabide depăşind 0,1 g.

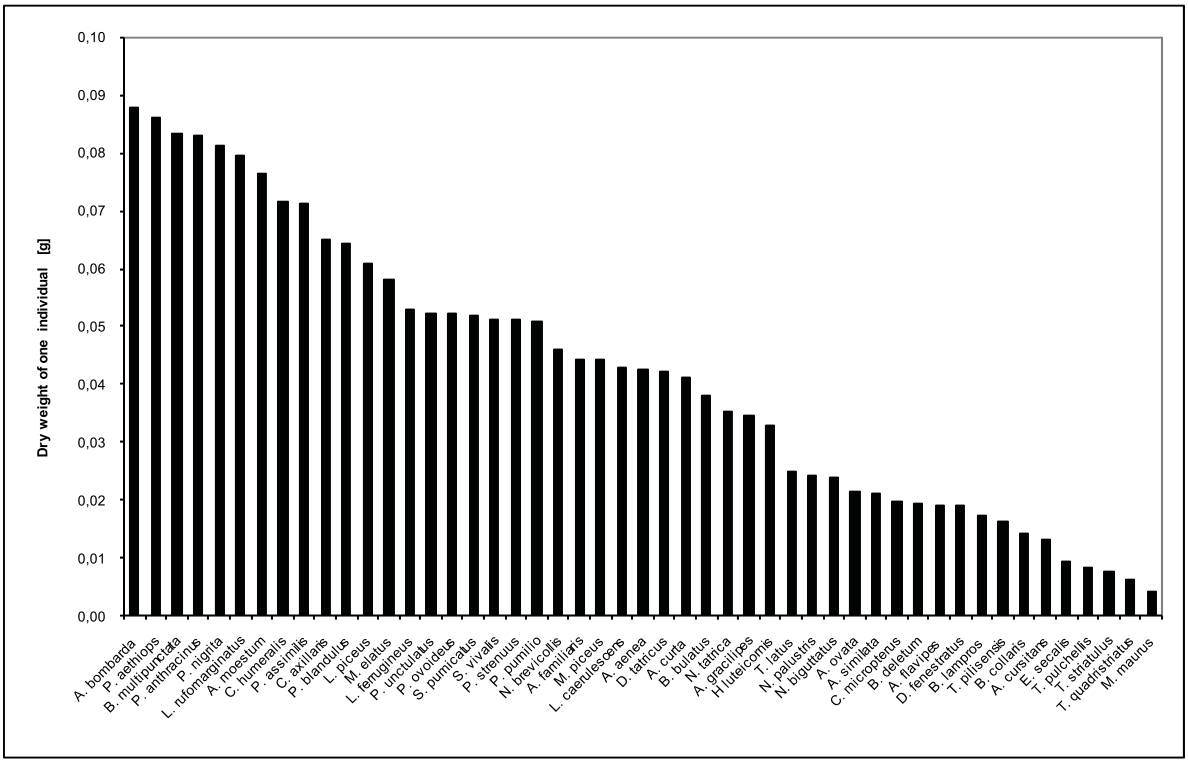

Figure 2. Average weight of Carabids species with the weight bellow 0.1 g.
Figura 2. Greutatea medie a speciilor de carabide sub 0,1 g.

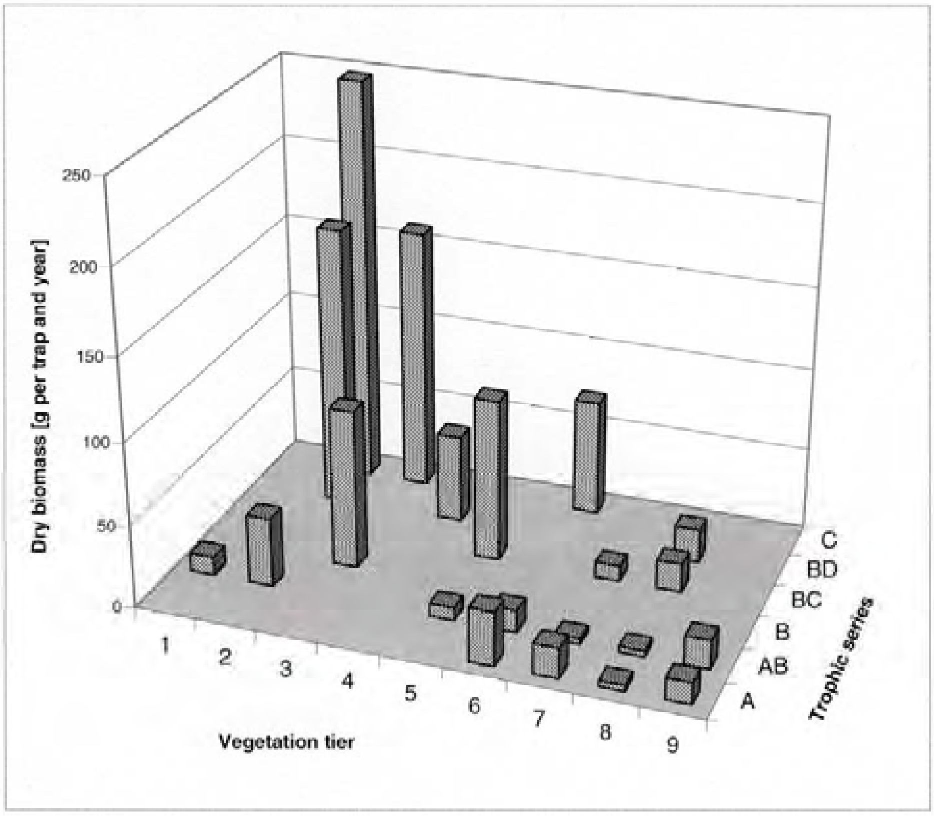

Figure 3. Average weight of dry biomass of carabid communities in different vegetation tiers and trophic series (1-9: oak vegetation tier-veg. tier of alpine meadows; A- acidophilous trophic series, B-neutral trophic series, C-nitrophilous trophic series, D-alkaline trophic series, AB, BD and BD-transitory trophic series).
Figura 3. Greutatea medie a biomasei uscate in cenozele de carabide în diferite zone de vegetaţie şi serii trofice (1-9: zona de vegetaţie a stejarului - zona de vegetaţie a pajiştilor alpine; A-serie trofică acidofilă, B-serie trofică neutrală, C-serie trofică nitrofilă, D-serie trofică alcalică, AB, BC şi BD-serii trofice de tranziţie).

The productivity of carabid communities in the individual trophic series and vegetation tiers is obviously very variable, as between these two categories (Fig. 3), as within them (Fig. 5). The extreme values are 300 g per trap and season (Pavlovské kopce, beech-oak vegetation tier, neutral-alkaline trophic series, *Querci Fageta*) and 0.9 g per trap and season (High Tatra, spruce vegetation tier, acid-alkaline series, *Sorbi abieti piceeta*). However, there are evident two clear tendencies: A decrease two directions-from the average values of almost 220-250 g per trap and year in the nitrophilous trophic series and in the beech-oak or oak-beech vegetation tier to average values of about 5-30 g per trap and year in the acidophilous trophic series and in the vegetation tiers of dwarf pines and alpine meadow. There exists a relatively high correlation between trophic series and cumulative dry biomass of the community (r = 0.68), while correlation between trophic series and number of individuals is lower (r = 0.55). The dry biomass of some communities, especially of those in higher altitudes is, however, in a contradiction (r = 0.47) with cumulative number of individuals (Fig. 4).

It is due to huge amounts of small species, especially *Pterostichus pumilio, Pterostichus unctulatus* and species of the genus *Trechus* in acidophilous spruce forests and a low quantitative representation or even absence of large species. In such cases, the low secondary production does not result only from little fertile substrate and, as a consequence, low food offer, but also from character of the litter or covering the ground surface or from a continuous growth of mosses, which make difficult movement or burying activity of large Carabids. On the contrary, in the most productive communities in low vegetation tiers and in the trophic series BD, BC and C, the high productivity and a relatively reduced number of individuals (Fig. 4) is caused by the predominance of *Carabus coriaceus* and/or of the species with average weight of one individual of 1.5-2.0 g (Table 1).

Especially in the habitats on the limestone or dolomitic limestone substrates (they do not mostly belong to the alkaline trophic series D, but in dependence of the terrain relief they belong to the nitrophilous series C or to the transitory series BD), the high productivity often results from high levels of carbonates in the soil making favourable conditions for mollusks. Their high abundance represents a rich food offer for large *Carabus* species. Within the material examined in this study it is particularly the case of all habitats in the Pavlovské kopce hills. On the contrary, the mollusks are almost absent on the acidophilous substrates, especially in the mountain forests of High Tatras of Malá Fatra.

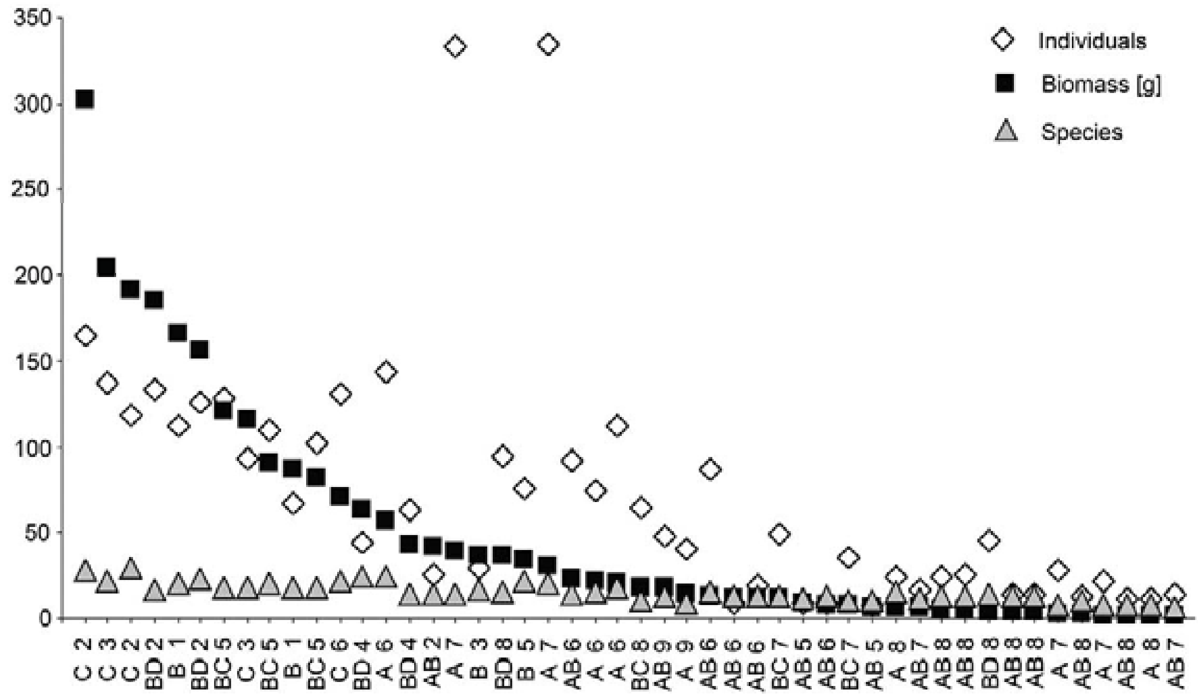

Figure 4. Dry biomass in grams, number of individuals and number of species of carabid communities in different vegetation tiers and trophic series, (abbreviations as in Fig. 3).
Figura 4. Greutatea medie a biomasei uscate în grame, numărul indivizilor şi a speciilor în cenozele de Carabidae în diferite zone de vegetație şi serii trofice (abrevieri ca în figura 3).

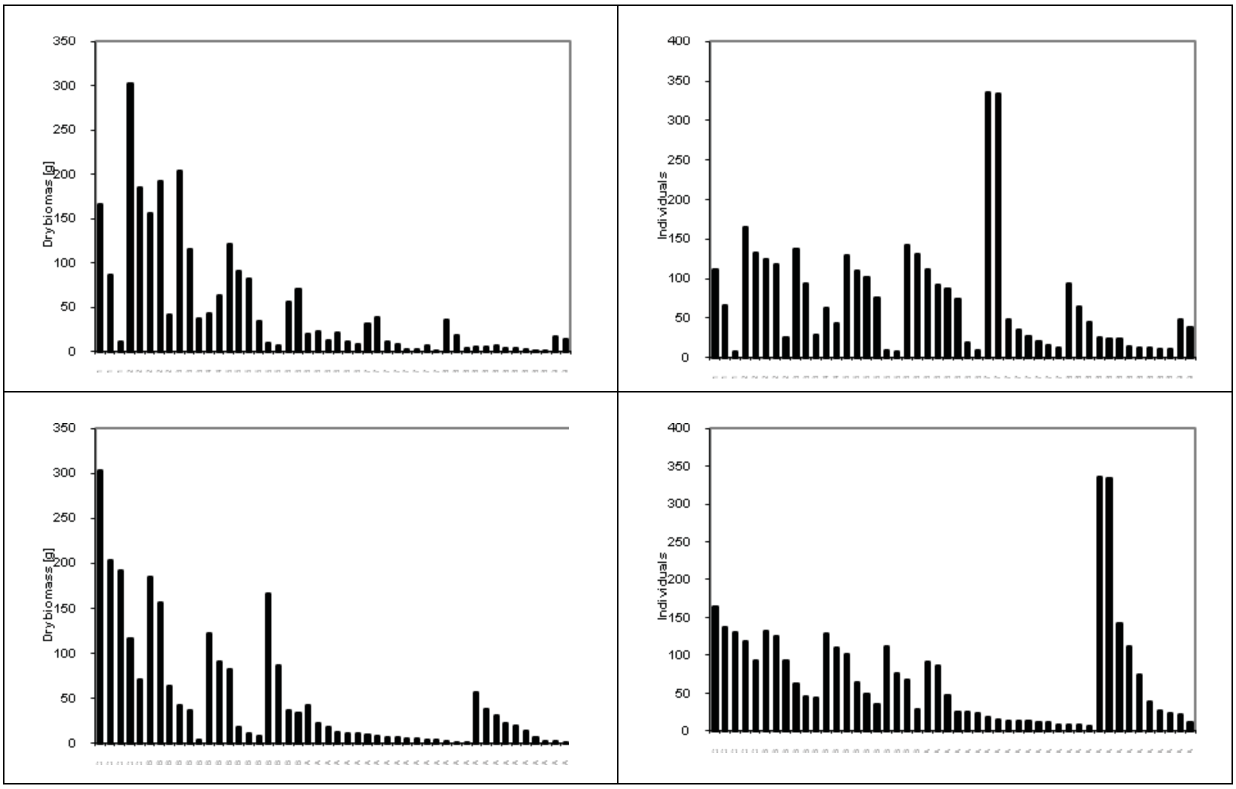

Figure 5. Variability of dry biomass and number of individuals with each trophic series and vegetation tier (abbreviations as in Fig. 3).
Figura 5. Variabilitatea biomasei uscate şi a numărului de indivizii în cadrul fiecărei serii trofice şi a zonei de vegetaţie (abrevieri ca în figura 3).

Table 1. Survey of localities.
Tabel 1. Lista localităţilor.

Locality	Part of transection	Year of sampling	Group of geobiocoens	Vegetation tier	Trophical series	Number of traps
Pavlovské vrchy		1981	CaQ	1	B	10
Pavlovské vrchy		1971	CaQ	1	B	10
Pavlovské vrchy		1981	TAc inferiora	2	C	10
Pavlovské vrchy		1971	TAc inferiora	2	C	10
Pavlovské vrchy		1981	FQ	2	B	10
Pavlovské vrchy		1971	FQ	2	B	10
Boleradice		1971	FQ	2	B	6
Pavlovské vrchy		1981	TAc superiora	3	C	10
Pavlovské vrchy		1971	TAc superiora	3	C	10
Buchlovice		1971	QF	3	B	6
Malá Pleš		1980	QF	4	BD	5
Kohoutov		1980	Fp	4	BD	10
Šrámková	32 - 40	1982	FAc	5	BC	8
Šrámková	L 10 - 13	1982	FAc	5	C	4
Šrámková	41 - 47	1982	FAc	5	BC	7
Šrámková	1 - 12	1982	FA	5	B	12
Žákova hora		1970	FA	5	AB	
Žákova hora		1971	FA	5	AB	10
Šrámková	24 - 32	1982	FAc	6	C	9
Šrámková	13 - 19	1982	PiAb	6	A	7
Kľačianska Magura	1 - 3	1984	FA	6	AB	3
Hřebínek	1 - 6	1980	SPi	6	AB	6
Kľačianska Magura	27 - 32	1984	FA	6	AB	5
Kľačianska Magura	20 - 26	1984	FAc	6	BC	8
Františkova Myslivna		1970	FA	6	AB	
Františkova Myslivna		1971	FA	6	AB	10
Kľačianska Magura	4 - 10	1984	AcPi	7	A	7
Kľačianska Magura	11- 19	1984	Spi	7	A	8
Kolové pleso		2006	Spi	7	BC	6
Kolové pleso		2006	Spi	7	BC	6
Zadné Meďodoly		2005	SPi	7	AB	6
Zadné Meďodoly		2005	SPi	7	A	12

Zadná javorová dolina		2005	Spi	7	AB	6
Zadné Meďodoly		2004 - 2006	Pm	8	BD	18
Kraková hoľa		2006	Pm	8	BC	6
Zadné Meďodoly		2005	Pm	8	BD	6
Zadné Meďodoly		2003 - 2006	Pm	8	A	18
Zadná javorová dolina		2005	Pm	8	AB	6
Kolové pleso		2005	Pm	8	AB	6
Kráľova hoľa		2006	Pm	8	AB	6
Zadná javorová dolina		2005	Pm	8	A	6
Zadná javorová dolina		2005	Ljt	9	AB	6
Zadná javorová dolina		2005	Ljt	9	A	6
Kráľova hoľa		2005	Ljt	9	AB	6
Ďumbier		2006	Ljt	9	AB	6
Ďumbier		2006	Pm	9	AB	6

Explanations:
Groups of greobiocoens:AcPi – *Aceri Pineta*, *CaQ – Carpini Querceta,* FAc – *Fagi Acereta, FQ – Fagi* Querceta, QF – *Querci Fageta*, PiAb – *Pini abiettea,* Pm *Pineta mugho*, Spi – *Sorbi Pineta,* TAc – *Tiliae Acereta*,
Vegetation tiers: 1 – oak veg. tier, 2 – beech-oak veg. tier, 3 – oak-beech veg. tier, 4 – beech veg. tier., 5 – beech-fire veg. tier, 6 – spruce-beech-fire veg. tier, 7 – spruce veg. tier, 8 – dwarf pine veg. tier, 9 – alpine meadows.

Table 2. Average dry weight of one individual of Carabid species (arranged alphabetically).
Tabel 2. Greutatea uscată medie a unui individ de carabidele (specii aranjate alfabetic).

Species	**Weight [g]**	**Species**	**Weight [g]**
Abax ovalis (DUFTSCHMIDT, 1812)	0.6283	*Harpalus luteicornis* (DUFTSCHMIDT, 1812)	0.0329
Abax paralelopipedus (PILLER ET MITTERPACHER, 1783)	1.1521	*Harpalus punctulatus* (DUFTSCHMIDT, 1812)	0.1390
		Harpalus quadripunctatus DEJEAN, 1829	0.1012
Abax parallelus (DUFTSCHMIDT, 1812)	0.5140	*Harpalus rufipalpis* STURM, 1818	0.1128
Agonum moestum DUFTSCHMID, 1812	0.0764	*Harpalus tardus* (PANZER, 1797)	0.1693
Agonum gracilipes (DUFTSCHMIDT, 1812)	0.0346	*Chlaenius tristis* (SCHALLER, 1783)	0.4236
Amara aenea (DE GEER, 1774)	0.0424	*Leistus ferrugineus* (LINNAEUS, 1758)	0.0501
Amara curta DEJEAN,1828	0.0413	*Leistus piceus* FROELICH, 1799	0.0610
Amara cursitans ZIMMERMANN. 1832	0.0206	*Leistus rufomarginatus* (DUFTSCHMIDT, 1812)	0.0795
Amara eurynota (PANZER, 1797)	0.0457	*Licinus hoffmannsegi* (PANZER, 1803)	0.1458
Amara familiaris DUFTSCHMIDT, 1812	0.0444	*Lorocera caerulescens* (LINNAEUS, 1758)	0.0428
Amara ovata (FABRICIUS, 1792)	0.0213	*Microlestes maurus* (STURM, 1827)	0.0041
Amara similata (GYLLENHALL, 1810)	0.0211	*Molops elatus* (FABRICIUS, 1801)	0.0582
Aptinus bombarda (ILLIGER, 1800)	0.0879	*Molops piceus* (PANZER, 1793)	0.0443
Asaphidion flavipes (LINNAEUS, 1764)	0.0192	*Nebria brevicollis* (FABRICIUS, 1792)	0.0459
Badister bulatus (SCHRANK, 1798)	0.0381	*Nebria tatrica* I. MILLER, 1859	0.0354
Bembidion lampros (HERBST, 1784)	0.0172	*Notiophilus biguttatus* (FABRICIUS, 1779)	0.0240
Membidion deletum AUDINET-SERVILLE, 1821	0.0195	*Notiophilus palustris* (DUFTSCHMIDT, 1812)	0.0241
Blethisa multipunctata (LINNAEUS, 1758)	0.0834	*Ophonus azureus* (FABRICIUS, 1775)	0.1002
Bradycelus collaris (PAYKULL, 1798)	0.0142	*Ophonus rufibarbis* (FABRICIUS, 1792)	0.1001
Calathus metallicus DEJEAN, 1828	0.1403	*Platynus assimilis* (PAYKULL, 1790)	0.0713
Calathus micropterus (DUFTSCHMIDT, 1812)	0.0196	*Poecilus cupreus* (LINNAEUS, 1758)	0.2710
Calosoma inquisistor (LINNAEUS, 1758)	1.6412	*Poecilus lepidus* (LESKE, 1787)	0.1827
Carabus arvensis HERBST, 1784	1.0965	*Pseudoophonus rufipes* (DE GEER, 1774)	0.4126
Carabus auronitens FABRICIUS, 1792	1.3251	*Pterostichus aethiops* (PANZER, 1797)	0.0862
Carabus cancelatus ILLIGER, 1758	1.3600	*Pterostichus anthracinus* (ILLIGER, 1798)	0.0831
Carabus convexus FABRICIUS, 1775	1.1212	*Pterostichus blandulus* I. MILLER, 1859	0.0643
Carabus coriaceus LINNAEUS, 1758	6.5950	*Pterostichus burmeisteri* (HEER, 1801)	0.1546
Carabus fabricii PANZER, 1813	1.1013	*Pterostichus cordatus* LETZNER, 1847	0.0953
Carabus glabratus PAYKULL, 1790	1.7215	*Pterostichus foveolatus* (DUFTSCHMIDT, 1812)	0.2152
Carabus hortersis LINNAEUS, 1758	1.7800	*Pterostichus melanarius* (ILLIGER, 1798)	0.5336
Carabus irregularis FABRICIUS, 1792	1.1241	*Pterostichus melas* (CREUTZER, 1799)	0.6421
Carabus linnei PANZER, 1813	1.0568	*Pterostichus morio* DUFTSCHMIDT, 1812	0.2322
Carabus nemoralis MÜLLER, 1764	1.7370	*Pterostichus niger* (SCHALLER, 1783)	1.0600
Carabus obsoletus STURM, 1815	1.9821	*Pterostichus nigrita* (PAYKULL, 1790)	0.0812

Carabus scheidleri PANZER, 1799	2.1885	*Pterostichus oblongopunctatus* (FABRICIUS, 1787)	0.1941
Carabus sylvestris PANZER, 1793	1.1216	*Pterostichus ovoideus* (STURM, 1824)	0.0521
Carabus ullrichi GERMAR, 1824	1.5132	*Pterostichus pilosus* (HOST, 1789)	0.6352
Carabus violaceus LINNAEUS, 1758	1.7457	*Pterostichus pumilio* (DEJEAN, 1828)	0.0410
Cychrus attenuatus (FABRICIUS, 1792)	0.9125	*Pterostichus strenuus* (PANZER, 1797)	0.0511
Cychrus caraboides (LINNAEUS, 1758)	0.9256	*Pterostichus unctulatus* (DUFTSCHMIDT, 1812)	0.0523
Cymindis axillaris (FABRICIUS, 1794)	0.0652	*Stomis pumicatus* (PANZER, 1796)	0.0520
Cymindis humeralis (FOURCROY 1785	0.0715	*Synuchus vivalis* (OLLIGER, 1798)	0.0512
Deltomerus tatricus (I. MILLER, 1859)	0.0421	*Trechus latus* PUTZEYS, 1846	0.0248
Dromius fenestratus (FABRICIUS, 1794)	0.0192	*Trechus pilisensis* CSIKI, 1918	0.0163
Epaphius secalis (PAYKULL, 1790)	0.0092	*Trechus pulchellis* Putzeis, 1846	0.0082
Harpalus atratus LATREILLE, 1804	0.1561	*Trechus quadristriatus* (SCHRANK, 1781)	0.0062
Harpalus distinguendus (DUFTSCHMIDT, 1812)	0.1873	*Trechus striatulus* PUTZEYS, 1847	0.0076
Harpalus latus (LINNAEUS, 1758)	0.1773	*Trichotichnus laevicollis* (DUFTSCHMIDT, 1812)	0.1431

Influence of the geological substrate of the secondary productivity and species composition of Carabids is not evident only from comparison of samples from remote localities, but can be directly observed in some parts of the West Carpathians, where a mosaic of acid or alkaline substrates exists on a small territory and their boundaries can be observed in the terrain ŠUSTEK (2006), ŠUSTEK & ŽUFFA (1986, 1988).

CONCLUSIONS

The maximum productivity of Carabid communities reaches 300 g per trap and vegetation season, while the minimum productivity drops to 1.6 g per trap and vegetation season. It is very variable, as within individual trophic series and vegetation tiers, as between them. The variation ranges within individual trophic series or vegetation tiers overlap mutually. But there is a general tendency of decreasing of productivity from the average values of 220-280 g per trap and vegetation season in the nitrophilous or transitory neutral – alkaline trophic series and lower vegetation tiers to 5-30 g per trap and vegetation season in the acid trophic series and mountain vegetation tiers. The average values of productivity in a richer trophic series are mostly visibly higher than those in the next poorer series. The secondary productivity expressed by the dry biomass is freely correlated with the productivity expressed by the cumulative number of individuals. In the more productive communities, a lower number of individuals of large species bind the major part of biomass, whereas in the less productive communities the existing biomass is split among a large number of individuals of small species. This relation is, however, strongly biased by character of litter and covering of soil surface by mosses, which create conditions for movement of individual species through the litter and hiding in it. Number of individuals can be generally used as an indicator of secondary productivity of Carabid communities, but it is to be always interpreted in regard with body size structure of the communities. Otherwise it can lead to misinterpretations.

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