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## AN ATTEMPT TO CHARACTERIZE MATTER TRANSFER BY CARABID COMMUNITIES INHABITING FORESTS\*

**ABSTRACT:** Matter transfer by zoophagous carabid' communities was studied in three forest habitats differing in respect of participation of spring and autumn breeders in the biomass production of the carabid community. Prevalence of biomass production of autumn breeders over that of spring breeders caused a relatively low rate of matter transfer, and small energy loss per unit of the community biomass production, as compared with the community in which spring breeders participated most in such production. The entire amount of biomass transferred by the community to the subsequent trophic levels was independent of the ratio of the autumn to the spring breeder production.

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### 1. INTRODUCTION

As far as abundance and biomass are taken into account, carabids are one of the dominant groups among the zoophages inhabiting the forest floor (Kaczmarek 1963, Zimka

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1966, Obrtel 1971 and others). They are often regarded as a factor controlling numbers of phytophagous species of insects (Scherney 1955, Šarova 1958, Grigoreva 1965, Titova and Žavoronkova 1965, Szyszko 1974), and favouring maintenance of ecological balance in forest ecosystems (Kaczmarek 1963). On the other hand, the zoophagous carabids inhabiting forests seem to be a link in the food-chain beginning with that part of the primary production which is transferred to macrosaprophages (Grüm 1976). Hence, their role as a factor controlling numbers of phytophagous insects may be of secondary importance.

To obtain a more complete outline of the role of zoophagous carabids in forests it is necessary to take into consideration their participation in energy flow and matter transfer. The aim of the present paper is to evaluate whether or not there are any features of the communities of zoophagous carabids inhabiting forests, that affect the amount, rate and direction of the matter transferred by the carabids.

The investigations were carried out in the Kampinos Forest (several kilometers north-west of Warsaw) in the years 1956 till 1974. The methods and results concerning biomass production of the carabids were the subject of separate publications of the present author (Grüm 1975a, 1975b, 1976), and now form the basic material for estimates of matter transfer.

## 2. STRUCTURE OF CARABID COMMUNITIES

Both structure of carabid communities and their productivity were studied in the following three forest habitats: (1) *Vaccinio myrtilli-Pinetum* (site symbol *VmP*) that covered a relatively dry homogeneous area of several hectares; (2) *Vaccinio myrtilli-Pinetum* (site symbol *P*) of about 0.2 ha in area surrounded by alder woods, and hence not so dry; (3) an area of about 4 ha (site symbol *PA*) composed mostly of dry (*Pino-Quercetum*) and wet (*Circaeo-Alnetum*) patches.

In the study period, 25 species of carabids were captured in pitfalls in the *VmP* site, 31 species in the *P* site, and 42 species in the *PA* site (Table I). Domination structure in the communities from these sites – expressed by percentage participation of separate species in the biomass production of the community (Fig. 1) – revealed a highly dominant species in the *VmP* site (*Carabus arcensis* – 64.5% of the entire biomass production) and in the *P* site (*Pterostichus niger* – 67.1% of the production). In the *PA* site, the most productive species (*P. niger*) was responsible for 31.6% of the community production. Spring breeders (Larsson 1939), i.e., the species with summer larvae, were responsible for 88% of the entire biomass production of the community dwelling in the *VmP* site. Contrary to that, autumn breeders (Larsson 1939), i.e., the species with winter larvae, produced 79% of the entire biomass production of carabids in the *P* site, and 74% in the *PA* site.

Hence, the carabid community in the *VmP* site shows a relatively simple structure (the lowest number of captured species, and presence of a highly dominating species) with prevalence of spring breeders in the biomass production. The community studied in the *P* site reveals a slightly more complex structure – because of a higher number of species captured – and prevalence of autumn breeders in the biomass production. In the carabid community of the most complex structure – expressed by the highest number of captured species and lack of a highly dominating species – namely that inhabiting the *PA* site, the biomass production of the autumn breeders also prevailed over that of spring breeders.

Table I. Species composition of the communities studied

No.	Species or genus	Site		
		VmP	P	PA
1	<i>Calosoma inquisitor</i> (L.)			+
2	<i>Carabus coriaceus</i> L.		+	+
3	<i>C. violaceus</i> L.	+		+
4	<i>C. clatratus</i> L.		+	+
5	<i>C. granulatus</i> L.		+	+
6	<i>C. arcensis</i> Hbst.	+	+	+
7	<i>C. nemoralis</i> Müll.	+	+	+
8	<i>C. hortensis</i> L.	+	+	+
9	<i>C. glabratus</i> Payk.		+	+
10	<i>C. nitens</i> L.	+		
11	<i>C. cancellatus</i> Ill.			+
12	<i>Cychrus caraboides</i> (L.)	+	+	+
13	<i>Nebria brevicollis</i> (F.)			+
14	<i>Leistus ferrugineus</i> (L.)	+	+	+
15	<i>Notiophilus</i> sp.	+	+	+
16	<i>Blethisa multipunctata</i> (L.)			+
17	<i>Elaphrus cupreus</i> Duft.			+
18	<i>Loricera caerulescens</i> (L.)	+	+	+
19	<i>Dyschirius globosus</i> (Hbst.)	+	+	+
20	<i>Asaphidion flavipes</i> (L.)		+	+
21	<i>Bembidion</i> sp.	+	+	+
22	<i>Epaphius secalis</i> (Payk.)	+	+	+
23	<i>Patrobus atrorufus</i> (Strom)		+	+
24	<i>Stomis pumicatus</i> (Panz.)			+
25	<i>Pterostichus oblongopunctatus</i> (F.)	+	+	+
26	<i>P. niger</i> (Schall.)	+	+	+
27	<i>P. vulgaris</i> (L.)	+	+	+
28	<i>P. anthracinus</i> (Ill.)			+
29	<i>P. nigrata</i> (F.)	+	+	+
30	<i>P. caerulescens</i> (L.)	+		
31	<i>P. aterrimus</i> (Hbst.)			+
32	<i>P. brunneus</i> (Sturm.)		+	+
33	<i>Calathus erratus</i> (Sahlbg.)	+	+	+
34	<i>C. micropterus</i> (Duft.)	+	+	+
35	<i>Agonum moestum</i> (Duft.)		+	+
36	<i>A. obscurum</i> (Hbst.)		+	+
37	<i>A. gracile</i> Sturm			+
38	<i>Badister peltatus</i> (Panz.)		+	+
39	<i>B. bipustulatus</i> (F.)			+
40	<i>Chlaenius tristis</i> (Schall.)			+
41	<i>Ch. nigricornis</i> (F.)	+		
42	<i>Bradycellus collaris</i> (Payk.)	+	+	+
43	<i>Acupalpus</i> sp.		+	
44	<i>Masoreus wetterhalli</i> (Gyll.)	+	+	+
45	<i>Metabletus truncatellus</i> (L.)	+	+	+
46	<i>Microlestes minutulus</i> (Goeze)	+	+	+
47	<i>Cymindis</i> sp.	+		
	Σ	25	31	42

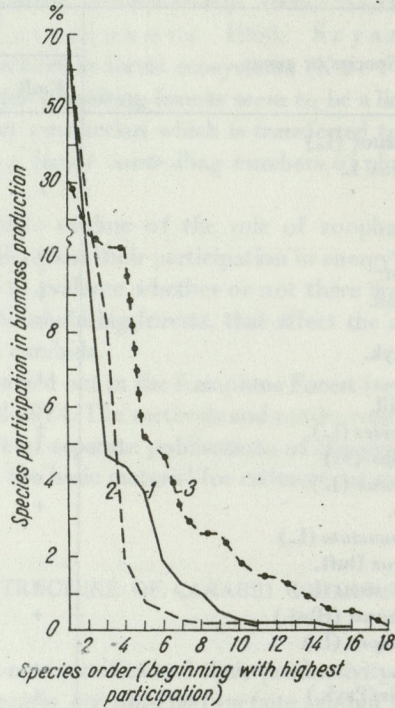


Fig. 1. Species domination structure  
1 - P site, 2 - VmP site, 3 - PA site

### 3. COMPONENTS OF MATTER TRANSFER

#### 3.1. Amount of biomass transferred

The entire biomass production of a carabid community is regarded here as the amount of biomass transferred to higher predators and scavengers.

The distinguished structural features, i.e., number of species, species domination structure and participation of a development type in the community production, do not seem to correlate with the entire biomass production of the community. Namely, the community of the simplest structure, inhabiting the VmP site, was characterized by the mid values of biomass production (Table II). Biomass production of the carabid community inhabiting the P site, i.e., the community of a slightly more complex structure, was the lowest, and the community of the most complex structure (in the PA site) produced the highest amount of biomass (Table II). Also, participation of a development type in the biomass production shows no relations with the entire biomass production of the community: high participation of autumn breeders in the biomass production (79% and 74%) was found in the communities of the lowest (P) and the highest (PA) entire biomass production (Table II).

Table II. Components of matter transfer

Parameters	Site		
	<i>P</i>	<i>V<sub>mP</sub></i>	<i>PA</i>
Biomass production* (kg dry weight · ha <sup>-1</sup> · yr <sup>-1</sup> )	0.766	0.942	1.321
Mean life-span (or immobilization time) (days)	126.9	87.9	135.4
<i>RMR</i> index (1 O <sub>2</sub> · ha <sup>-1</sup> · hr <sup>-1</sup> )	0.385	0.611	0.714
<i>AMR</i> index (kGm · ha <sup>-1</sup> · day <sup>-1</sup> )	1.463	1.954	2.573

\*Accepted after Grüm (1976)

### 3.2. Rate of biomass transfer

The biomass produced by a population is immobilized – i.e., not transferred – for the time defined by the mean life-span of the population members. The reciprocal of the immobilization time is a measure of the rate of biomass transfer by the population:

$$\bar{B} = P \bar{t}$$

where:  $\bar{B}$  – mean biomass,  $P$  – biomass production,  $\bar{t}$  – immobilization time. Hence, values of  $\bar{t}$  and  $\frac{P}{\bar{B}}$  are inversely proportional. This is a concept similar to biomass turnover, regarded as an index of efficiency of biomass production (Petrušewicz and Macfadyen 1970):

Table III. Comparison of mean life-span of individuals of different species

Development type	Species	Number of eggs deposited by female in the breeding season	Mean life-span of individuals (in days)
Spring breeders	<i>C. nemoralis</i>	10.6	146
	<i>C. clatratus</i>	20.3	98
	<i>C. arcensis</i>	23.5	90
	<i>C. granulatus</i>	23.7	90
	<i>A. moestum</i>	41.3	64
	<i>P. oblongopunctatus</i>	45.6	60
	<i>P. nigrita</i>	48.0	58
	<i>P. anthracinus</i>	93.9	39
Autumn breeders	<i>C. coriaceus</i>	7.7	282
	<i>C. violaceus</i>	22.9	198
	<i>C. hortensis</i>	26.1	190
	<i>C. glabratus</i>	30.0	181
	<i>C. caraboides</i>	32.0	178
	<i>P. atrofufus</i>	35.2	172
	<i>P. niger</i>	90.2	127
	<i>P. vulgaris</i>	91.1	126
	<i>C. erratus</i>	121.0	115
	<i>C. micropterus</i>	125.0	114

$$\theta = \frac{1}{t}$$

The immobilization time calculated for a carabid community should depend on its structure, because the mean life-span of individuals in populations of autumn breeders is usually longer than that in spring breeder populations (Grüm 1975a).

For 3 species of spring breeders (*Carabus arcensis*, *C. nemoralis* and *Pterostichus oblongopunctatus*) as well as for 3 species of autumn breeders (*C. glabratus*, *C. hortensis*, and *P. niger*), the relation between female fertility and life-span of individuals was estimated on the data taken from Grüm (1975b). The relation is expressed by a linear regression equation (Fig. 2). Substituting into the equation the data on female fertility accepted after Grüm (1976), the appropriate values for the mean life-span of individuals of the separate species under study were extrapolated (Table III).

The mean immobilization time of biomass produced by a community composed of  $i$  species is given by the formula:

$$\bar{t} = \frac{\sum_{k=1}^k P_k t_k}{\sum_{k=1}^k P_k}$$

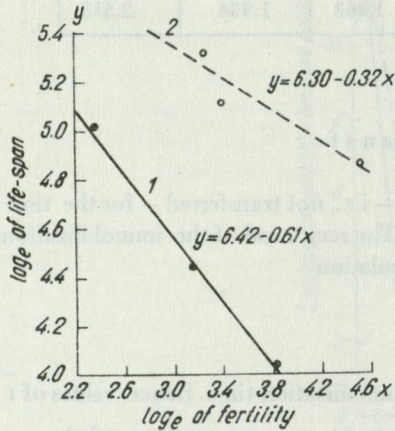


Fig. 2. Relation between mean life-span and female fertility

1 — spring breeders, 2 — autumn breeders

where:  $P_k$  — biomass production of  $k$ th species,  $t_k$  — life-span of individuals of  $k$ th species.

Mean immobilization time was relatively long in the case of the communities inhabiting the  $P$  and  $PA$  sites, in which mostly autumn breeders participated in the biomass production (Table II). Contrary to that, in the  $VmP$  site, in which biomass production of spring breeders highly prevailed over that of autumn breeders, the immobilization time was relatively short (Table II).

Thus, the rate of biomass transfer by carabid communities was relatively high in the site in which spring breeders predominated in the community biomass production ( $VmP$ ), and relatively low in the sites  $P$  and  $PA$ , where autumn breeders predominated. Other structures — like the number of species and species domination — did not seem to correlate with the rate of biomass transfer.

### 3.3. Resting metabolism rate

Resting metabolism rate ( $RMR$ ) of a species population is expressed here by an index, for the period in which individuals of the species gain their full weight and start to reproduce. This is the period that seems to be the most productive of all the periods in the individual's life, and moreover, the population biomass is highest at that time (Grüm 1975b).

The applied index of  $RMR$  is the product of the population biomass (in milligrammes dry weight per hectare) and  $O_2$  consumption at  $19^\circ C$  by the individual of the species involved,

calculated per milligramme dry weight per hour. The appropriate biomass values were taken from Grüm (1976).  $O_2$  consumption for most of the species under study was extrapolated from the formula:

$$y = 2.445 - 0.309 x$$

where:  $y$  —  $O_2$  consumption at  $19^\circ\text{C}$  in microlitres per milligramme dry weight per hour,  $x$  —  $\log_e$  of dry weight of an individual, in milligrammes (Fig. 3). This formula was derived from the data on oxygen consumption of the following 3 species differing in mean body weight: *C. coriaceus* (620.1 mg dry weight), *C. glabratus* (285.2 mg) and *P. niger* (81.7 mg).

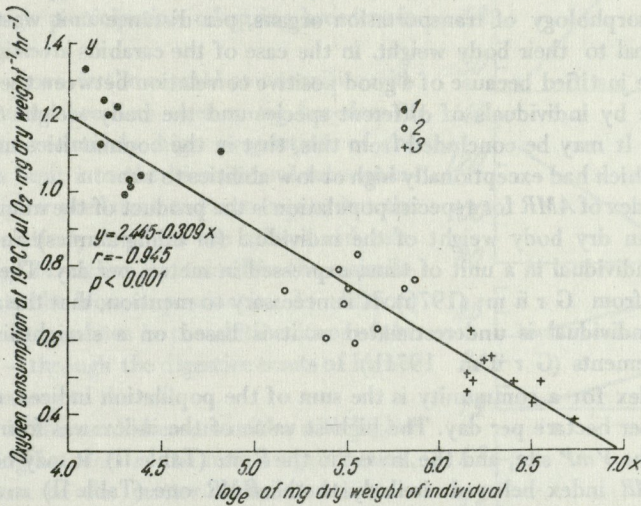


Fig. 3. Oxygen consumption by beetles of different body weight  
1 — *P. niger*, 2 — *C. glabratus*, 3 — *C. coriaceus*

The *RMR* index of a carabid community is the sum of the indices calculated for species populations, expressed in litres  $O_2$  per hectare per hour, at  $19^\circ\text{C}$ .

The community index of *RMR* was highest in the *PA* site, only slightly lower in the *VmP* site, and distinctly lower in the *P* site (Table II). The distinguished structural features of the communities do not seem to have any relation to the index. Namely, both the community of the simplest structure (in the *VmP* site) and that of the most complex (in the *PA* site) consumed almost the same amount of oxygen (Table II). Neither participation of autumn breeders in the community biomass production was connected with the index: high participation of autumn breeders in the production (the *P* and *PA* sites) was accompanied by the lowest and the highest value of the index (Table II).

The index is based on biomass values (community biomass at a specific moment and  $O_2$  consumption per a biomass unit). Hence, the relatively high *RMR* index in the *VmP* site can be evaluated by the relatively low mean body weight of individuals in this community (24.1 mg dry weight), as compared with the mean body weight of the individuals in the community inhabiting the *PA* site (78.6 mg dry weight).

### 3.4 Active metabolism rate

It is commonly known for insects that oxygen consumption of mobile individuals exceeds many times the consumption of resting ones. As far as carabids are concerned, daily consumption of  $O_2$  by an individual of average mobility and active only during the night is at least twice as high as daily  $O_2$  consumption of an individual resting all day (Grüm 1971a). Therefore, it seems to be important for productivity estimations to incorporate the energy wasted by mobility.

Energy loss in a species population, resulting from mobility of its members, was estimated also in the form of an index, for the same period for which the *RMR* estimates were made. The applied index of active metabolism rate (*AMR*) is based on the assumption, that individuals with a similar morphology of transportation organs, per distance unit waste an amount of energy proportional to their body weight. In the case of the carabids investigated, this assumption seems to be justified because of a good positive correlation between the distance covered in a unit of time by individuals of different species and the body weight of the individuals (Grüm 1976). It may be concluded from this, that in the communities under study, there were no species which had exceptionally high or low abilities to run.

The applied index of *AMR* for a species population is the product of the number of individuals per hectare, mean dry body weight of the individual (in milligrammes) and mean distance covered by the individual in a unit of time, expressed in meters per day. The appropriate data have been taken from Grüm (1976). It is necessary to mention, that the accepted distance covered by an individual is underestimated as it is based on a straight-line model of an individual's movements (Grüm 1971b).

The *AMR* index for a community is the sum of the population indices, expressed in kilogramme-meters per hectare per day. The highest value of the index was found in the *PA* site, the mid one in the *VmP* site, and the lowest in the *P* site (Table II). It may be concluded from this that the *AMR* index behaved similarly to the *RMR* one (Table II) and hence, was not connected with any of the distinguished structural features of the communities.

## 4. TRENDS IN AMOUNT, DIRECTION AND RATE OF MATTER TRANSFER

If the fact that higher biomass production is accompanied by higher indices of *RMR* and *AMR* (Table II) is taken into consideration, it is reasonable to conclude that consumption and biomass production are positively correlated. In forest ecosystems the entire biomass production of a community of zoophagous carabids seems to be positively correlated with the amount of nitrogen transferred by the primary producers to the saprophages dwelling in the soil and litter (Grüm 1976). Therefore one may suppose that there exists a more or less constant ratio between energy flow through the macrosaprophages and the carabids inhabiting forests.

The direction and rate of such transfer of matter consumed (or better assimilated) by the carabids seem to be dependent on one of the distinguishing structural features of the communities, namely, the ratio of the spring breeder production to the autumn breeder production.

In the communities with a prevalence of autumn breeders in the production of biomass, the indices of the community *RMR* and *AMR* are slightly lower per unit of biomass production, than those in the community with a prevalence of spring breeders (Fig. 4). Consequently, in the



former communities, the amount of energy wasted per a unit of biomass production is relatively low. This means that: (a) a relatively high percentage of the assimilated matter is being built into the biomass production and later transferred to higher predators and scavengers, (b) a relatively low percentage of assimilation is transferred to decomposers in the form of faeces.

As far as the rate of biomass transfer is concerned, in the communities with high participation of autumn breeders in the biomass production, the immobilization time of the biomass produced is relatively long (Fig. 4). Consequently, the rate of transfer of the biomass produced has to be relatively low. The opposite situation occurs in the communities with high participation of spring breeders in the biomass production.

Summing up the above, in the carabid communities with a prevalence of autumn breeders over spring breeders in biomass production, a relatively high proportion of the assimilated matter is built into the biomass and subsequently transferred to higher predators and scavengers, but the rate of transfer is relatively low. On the other hand, relatively high percentage of carbon contained in the assimilated matter is built into the biomass production. In addition, most of the carbon accumulates in the chitine cover of the carabids, and hence – through the digestive tracts of higher consumers – finds its way to the soil.

Contrary to that, in the carabid communities with higher participation of spring breeders in the biomass production, a relatively small part of the matter assimilated is transferred to higher consumers, but the rate of the transfer is relatively high. Coming back to the question of carbon transfer, in these communities a relatively large part of this component contained in the assimilated matter is delivered to the atmosphere, and not to the soil.

It seems to be especially significant, that spring breeders predominate in forest carabid communities from poor soils, while the communities from rich soils are characterized by a prevalence of autumn breeders (S z y s z k o 1974). This may indicate, that relatively more intensive transfer of carbon to the atmosphere – favouring soil mineralization – takes place in the carabid communities from poor soils. Contrary to that, rich soils inhabited by the carabid communities with a prevalence of autumn breeders seem to be relatively better supplied with the carbon transferred by carabids, that may support soil humification.

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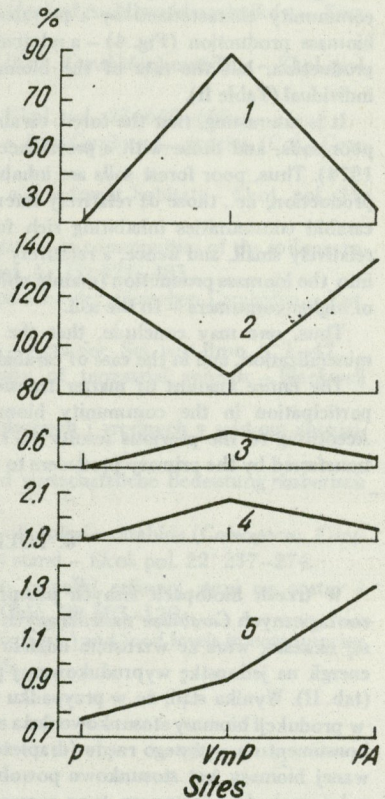


Fig. 4. Indices of rate of matter transfer  
 1 – participation of spring breeders in biomass production,  
 2 – immobilization time (days),  
 3 – RMR per biomass production,  
 4 – AMR per biomass production,  
 5 – biomass production (kg dry weight · ha<sup>-1</sup> · yr<sup>-1</sup>)

## 5. SUMMARY

The investigations – carried out in 3 forest habitats – indicate, that in the communities of zoophagous carabids in which autumn breeders predominate over spring breeders in the biomass production, mean life-span of the individual is relatively long (Table II), and the amount of energy lost per unit of biomass production is relatively small (Fig. 4). Consequently, in the communities with a predomination of autumn breeders, a relatively large part of the assimilated matter is built into the biomass production and transferred to higher consumers (predators and scavengers), but the rate of the transfer is relatively low. In the community characterized by a prevalence of spring breeders – because of higher energy loss per unit of biomass production (Fig. 4) – a relatively small part of the assimilated matter is built into the biomass production, but the rate of the biomass transfer is higher, as indicated by the shorter life-span of the individual (Table II).

It is interesting, that the forest carabid communities with a prevalence of spring breeders inhabit usually poor soils, and those with a prevalence of autumn breeders dwell in habitats with rich soils (S z y s z k o 1974). Thus, poor forest soils are inhabited by carabid communities of high energy loss per unit of biomass production, i.e., those of relatively intensive transfer of carbon to the atmosphere. Contrary to that, in the carabid communities inhabiting rich forest soils, the energy losses per unit of biomass production are relatively small, and hence, a relatively large part of the carbon contained in the assimilated matter is built into the biomass production (mainly chitine cover of the body) and transferred – through the digestive tracts of higher consumers – to the soil.

Thus, one may conclude, that the matter transferred by carabids from poor forest soils favours soil mineralization, and in the case of carabids from rich soils, supports soil humification.

The entire amount of matter transferred by carabids inhabiting forests is independent of whether the participation in the community biomass production is mainly by spring or autumn breeders (Fig. 4). According to the previous results (G r ü m 1976), this is roughly proportional to the amount of nitrogen transferred by the primary producers to the litter saprophages.

## 6. POLISH SUMMARY (STRESZCZENIE)

W trzech biotopach leśnych przeprowadzono badania nad wpływem struktury gatunkowej zespołów zoofagicznych *Carabidae* zasiedlających ściółkę na charakterystykę przekazywania materii przez zespół. Jak się okazało, wraz ze wzrostem udziału gatunków reprezentujących jesienny typ rozwojowy spadają straty energii na jednostkę wyprodukowanej przez zespół biomasy (fig. 4) i rośnie przeciętny czas życia osobnika (tab. II). Wynika stąd, że w przypadku zespołów z przewagą udziału gatunków jesiennego typu rozwojowego w produkcji biomasy stosunkowo duża część zasymilowanej materii zostaje wbudowana w biomasę i przekazana konsumentom wyższego rzędu (drapieżcom, padlinozercem), przy czym tempo przekazywania wyprodukowanej biomasy jest stosunkowo powolne. Natomiast w zespole cechującym się przewagą udziału gatunków należących do wiosennego typu rozwojowego w produkcji biomasy zespołu, stosunkowo mała część zasymilowanej materii zostaje wbudowana w produkcję – co wynika ze znacznych strat energii na jednostkę wyprodukowanej biomasy (fig. 4) – ale tempo przekazywania wyprodukowanej biomasy do wyższych poziomów troficznych jest szybsze, na co wskazuje przeciętnie krótki czas życia osobnika (tab. II).

Warto podkreślić, że w zespołach *Carabidae* zasiedlających ubogie gleby leśne dominują zwykle gatunki należące do wiosennego typu rozwojowego, a w zespołach zasiedlających gleby bogate – gatunki jesiennego typu rozwojowego (S z y s z k o 1974). Tak więc gleby ubogie zasiedlane są na ogół przez zespoły cechujące się dużymi stratami energii w przeliczeniu na jednostkę wyprodukowanej biomasy, to znaczy intensywnym przekazywaniem do atmosfery węgla zawartego w zasymilowanym pokarmie. W przeciwieństwie do tego, w zespołach *Carabidae* na bogatych glebach leśnych straty energii na jednostkę wyprodukowanej biomasy są względnie niskie, a w konsekwencji węgiel zawarty w zasymilowanym pokarmie jest w większym stopniu wbudowywany w produkcję biomasy (głównie chitynową okrywę ciała) i poprzez przewod pokarmowy konsumentów wyższego rzędu przekazywany do gleby.

Można na tej podstawie wysnuć wniosek, że przekazywanie materii przez zespoły *Carabidae* ma inny charakter na glebach ubogich – sprzyja mineralizacji, a inny na bogatych – sprzyja humifikacji. Należy tu dodać, że całkowita ilość materii przekazywanej przez *Carabidae* zasiedlające lasy nie zależy od proporcji między gatunkami należącymi do wiosennego i jesiennego typu rozwojowego (fig. 4), lecz jest skorelowana z

ilością azotu dochodzącego wraz z opadem listowia do ściółki leśnej, a więc z reguły wyższa na glebach bogatych (Grüm 1976).

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