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ANALYSIS OF A SHEEP PASTURE ECOSYSTEM IN THE PIENINY MOUNTAINS (THE CARPATHIANS) XVII. ANALYSIS OF THE TRANSFER OF CARBON*

ABSTRACT: The paper presents the results of 3 year investigations performed by a group of workers on the transfer of carbon through two trophic chains – the detritus chain and the grazing chain. The investigations were performed on two areas of a pasture differing in the amounts of organic fertilizers applied. 86% of the field layer plant production was found to be used by sheep. A very large part of the consumed mass returns to the ecosystem in the form of manure which decomposes much faster than unprocessed dead plant matter. Coprophages play an important role in the process of manure decomposition. After isolation from these animals the rate of manure decomposition decreased by almost one-half. In the soil manure causes an increase in the intensity of mineralization processes (increase of the biomass and respiration of several groups of soil organisms) as well as of humification processes (an increase in the production of earthworm coprolites and the abundant development of related bacteria). Intensive application of organic fertilizers was found to lead to simplification of the structure of the plant community and of several animal associations (*Lumbricidae, Formicidae, Acarina*).

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1. INTRODUCTION

The investigations discussed here were performed in the years 1969–1971 by a group of persons mainly from the Department of Grassland Ecosystems (Institute of Ecology) with collaboration of the Institute of Soil and Agriculture Chemistry (Warsaw Agricultural University) and the Department of Animal Evolution and Ecology (Warsaw University).

The aim of these investigations was to examine the main pathways of energy flow in pasture ecosystems differing in intensity of manuring and to monitor the whole process of changes which occur in an ecosystem directly after application of manure. An attempt was made to evaluate the energy flow through two trophic chains: (1) the detritus chain which includes the part of primary net production which remains in the pasture, is not used by herbivores and undergoes dying and decay, and (2) the grazing chain – or the subsequent stages of degradation of energy taken up by herbivorous animals.

An attempt was made to make the energy budget in the ecosystem and to oppose the amount of organic mass produced to the processes of respiration of organisms involved in the subsequent stages of degradation. It is important to stress that not only the effects of the transfers but also the organisms causing them were examined.

The experiment were performed on sheep pastures in the mountains of the Małe Pieniny range in southern Poland located 700 m above sea level and occupying an area which was previously cultivated.

The soil of these pastures was mainly formed from weathering of flysch rocks characteristic for the Carpathians. These are brown pseudogley soils with low amounts of available nitrogen and phosphorus. These pastures are included in the association *Lolio-Cynosuretum cristati* (Traczyk and Kochev 1974). More detailed data are given in Table I (Czerwiński and Tatur 1974a, Kostuch and Kuc 1973).

Tab. I. General characteristic of the investigation area

Slope of sites – 5°, exposition – southern, grazing season – May-Sept., average air temperature in 1970 – 5.7°C, average air temperature in the grazing season – 12.9°C, average soil temperature in the grazing season – 13.8°C, total rainfall in 1970 – 1160 mm

Sites	pH in H_2O	Soil properties				
		K_2O	P_2O_5	C (%)	N (%)	C/N
		(mg/100 g soil)				
Site *P*	5.8	8.5	0.8	2.09	0.232	9.0
Site *F*	5.8	53.0	0.8	2.95	0.317	9.3

The investigations were performed on areas of the pasture which differed in intensity of manuring and the length of time which passed since the moment of manuring (penning-up sheep). The area on which most of the investigations were concentrated, the so-called Owcza Droga (Sheep Way – site *P*) was constantly fertilized with small doses of about 2.4 g d.wt./m^2/d (360 g d.wt./m^2/season) during the daily passage of sheep. This corresponds to about 90 kg N/ha. Other areas on which sheep were penned-up were fertilized with large amounts of manure during a short period of time – about 170 g d.wt./m^2/d for 3 days (Olechowicz 1974) and subsequently after the passage of several weeks were supplied with the same doses of manure as the previous ecosystem (about 650 g d.wt./m^2/season). The process of penning-up sheep is repeated in the same place every 3 years.

The paper thus contains the comparison of two differently manured areas of a pasture in respect to the amount of carbon stored as plant production and its rate of flow.

The subsequent stages of the succession of organisms in the manure which takes place during several months from the manuring of the pasture is also presented.

2. THE TRANSFER OF CARBON IN A MODERATELY FERTILIZED ECOSYSTEM

2.1. Detritus food chain

The quantitative picture of the flow and retention of carbon at particular trophic levels in an area of pasture with relatively little manuring (site *P*) is presented in Figure 1.

The C content in meadow plants was taken as 42% dry mass (Cummins 1967, Ławacz unpubl.).

The net primary production was found to be 320 g C/m^2/year. Of this 81 g is produced by roots and belowground shoots and 239 g by the green parts of plants. The production of the above-ground parts is three times higher than that of the belowground ones according to these calculations (Andrzejewska 1974, Plewczyńska-Kuraś 1974).

The given value for the production of roots and belowground shoots corresponds to the difference between the maximal and minimal state of the biomass during the season. This value describes the minimal rather than the real production but due to the great difficulty in estimating the production of perennial meadow plants this method is commonly used (Kucera, Dahlman and Koelling 1967, Kotańska 1970, Sims and Singh 1971). The period of functioning of the main root mass determined by the method of Dahlman and Kucera (1965) is for this method of evaluating production approximately 3 years. Similar values are given by other authors who use this method of estimating production, however, Speidel and Weiss (1971) found much shorter periods using the method of direct observation of growth.

The whole below ground plant material was divided into two fractions – the so-called morphic fraction consisting of particles not smaller than 2 mm and the small detritus

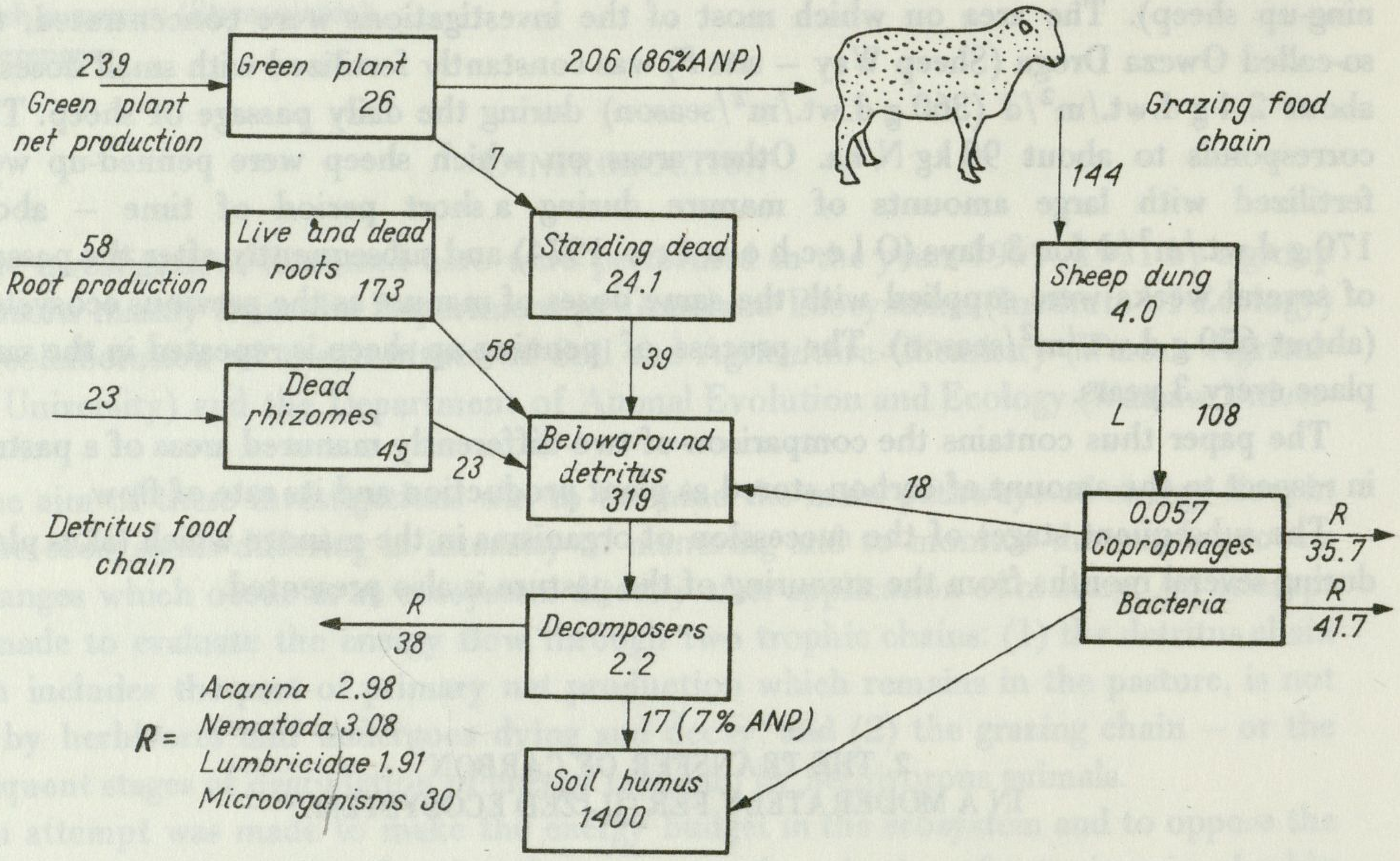

Fig. 1. Transfer of carbon is pasture ecosystem. Site *P*. Estimates for top 0–5 cm of soil, data for the year 1970 (based on Andrzejewska 1974, Breymeyer 1974, Czerwiński, Jakubczyk and Nowak 1974, Olechowicz 1974, Plewczyńska-Kuraś 1974, Wasilewska 1974, Nowak 1975, Żyromska-Rudzka unpubl.)

Transfer – g C/m^2/season, compartments – g C/m^2/season, *R* – respiration – g C/m^2/season, *L* – Weight loss (respiration + production) – g C/m^2/season, *ANP* – green plant net production

fraction with particles 0.25–2 mm (Plewczyńska-Kuraś 1974). The morphic fraction was sorted into parts of root and of shoot origin and an attempt was made to separate living and dead material. The content of organic matter in the detritus fraction was determined by ignition at 600°C. In the last fraction it was too difficult to separate dead and living material which may have contributed to some underestimation of the living mass of the roots.

The average root biomass is relatively very large (173 g C/m^2) which is much higher than the biomass of the above-ground parts which is 26 g C/m^2, that is 6 times lower.

In this work only the top 0–5 cm layer of the soil was analyzed. In this layer living matter is concentrated. It contains about 80% of the root mass and all of the nodes of propagation (average biomass 31.0 g C/m^2) and belowground shoots (45 g/C/m^2).

The detritus content in the soil is also very high, higher than that of morphic parts and is on the average 319 g C/m^2 in the top 5 cm layer of the soil (Plewczyńska-Kuraś 1974).

The estimation of the cost of respiration of the main groups of soil organisms which participate in the decomposition of dead plant material is based on the data on the mean biomass of organisms occurring in the examined area (J a k u b c z y k 1974b, Ż y r o m s k a-R u d z k a 1974, W a s i l e w s k a 1974, N o w a k 1975). These data were multiplied by appropriate respiration coefficients characteristic for each of the groups taken either from our own investigations or from the literature with correction for temperature (J e n s e n 1936, B e r t h e t 1964, L u x t o n and T h o m a s 1972, W o o d and L a w t o n 1973, W a s i l e w s k a 1974, N o w a k 1975).

In these calculations not all organisms were taken into account, but this does not seem to have any significant effect on the result obtained as just two of the groups taken into consideration – earthworms and microorganisms make up over 90% of the biomass of soil organisms (Tab. II).

Tab. II. Biomass of soil invertebrates and bacteria after manuring (mg d.wt./m^2) (data after D e l c h e v and K a j a k 1974, J a k u b c z y k 1974a, 1974b, P ę t a l 1974, W a s i l e w s k a 1974, N o w a k 1975)

Trophic groups		Pasture	Sheep-fold
Herbivores	*Elateridae*	219	850
	Nematoda	58.2	66.8
Decomposers	Earthworms	4.5×10^3	20.60×10^3
	Ammonifying bacteria	0.5×10^3	0.92×10^3
Predators	*Nematoda*	76.2	21.0
	Ants	52.3	3.5
	Spiders	4.2	2.6
Elimination of earthworms in per cent		22	13

The respiration of soil organisms amounts to 38 g C/m^2/year. Of this 30 g C/m^2/year is used by microorganisms and the remaining 8 g C/m^2/year by saprophagous animals (Fig. 1). This is a small value compared with the yearly influx of dead material which is, as was presented above, at least 120 g C/m^2/season.

If the given ecosystem is in a steady state this of equilibrium this means that the influx substances is counterbalanced by processes of decay and the dispersion of energy in the process of respiration almost counterbalances the influx of dead organic matter. With this assumption the respiration of soil organisms during 150 days of activity would be 0.8 g $C/m^2/d$ instead of the 0.27 g $C/m^2/d$ calculated previously (Fig. 1). Such high values reaching up to 1 g $C/m^2/d$ were obtained in the measurement of soil organism respiration in fertile mown meadows of the *Arrhenatheretum* type (Reuss 1971, Tesařová and Gloser 1972, Kubicka 1973). As the biomass of the organisms in the examined area is smaller than in meadows of this type it seems justified to assume that the values of respiration were not underestimated and that accumulation of organic matter in the soil is to be expected. In quoting data on the intensity of respiration of soil organisms it was taken after Kubicka (1973) that root respiration is 40% of the respiration of the whole soil monolith.

According to data given by Klapp (1962) an increase of organic substance in meadow soil is a normal phenomenon both in exploited and in natural unexploited areas such as prairies and steppes. Similarly data given by Reichle (in press) about prairies indicate that respiration of heterotrophs constitutes about 1/3 of the influx of plant material.

In recent large scale American experiments on of the flow of energy in grassland ecosystems it was shown that in most plant communities (14 out of 18 examined) the net production is greater than the decomposition and thus accumulation of organic matter takes place (Lewis 1971, Sims and Singh 1971). This is the case at least during the growing season. In those investigations only the growing season, in some cases very long (260 days) was taken into consideration. In about 1/3 of the examined grassland ecosystems the accumulation was considerable and exceeded 25% of the net production (29.5–57.0%). It thus seems probable that even during the whole year the decomposition does not counterbalance production.

The large content of detritus in the soil of the pasture in Jaworki which exceeds the influx of material two times (Fig. 1) indicates that the retention of a considerable part of the dead plant material does occur in the soil.It is a confirmation that at least during the vegetation season the influx of material into the soil is greater than its decay.

It is estimated that 17 g C per year passes from the soil detritus into the humus as a result of the activity of earthworms (Czerwiński, Jakubczyk and Nowak 1974). This amount is the excess of carbon content in coprolites which are produced during the year by earthworms over the average C content in the soil. The organic content of coprolites is similar to that of soil humus. Thus as a result of the action of earthworms about 7% of plant production is transformed into humus. This is probably not the only way of changing detritus into humus but it is at least one of the most important. In coprolites the processes of microbiological changes are faster and more intense than in control soil without earthworms (Czerwiński, Jakubczyk and Nowak 1974).

The following are characteristic for the detritus food chain in a pasture: (1) it is based mainly on the belowground plant mass; (2) the content of both living and dead parts of plants in the soil is relatively large (537 g C/m^2) as compared with the influx (120 g C/m^2/season); (3) earthworms (4.5 g d.wt./m^2) and bacteria (0.5 g d.wt./m^2) dominate in respect to biomass among the soil organisms; (4) processes of humus formation appear to be intensive; (5) respiration processes do not seem to counterbalance production processes and thus accumulation of organic matter in the soil takes place during the growing season.

2.2. The grazing food chain

Sheep were, of course, the main component of this chain. The consumption of plants by insects and other invertebrates is much smaller in a pasture than in meadows. The biomass of insects feeding on the above-ground parts of roots is only of the order of several mg/m^2. The biomass of belowground herbivores (*Nematoda, Elateridae*) is considerably greater – jointly 277 mg d.wt./m^2 (Tab. II) (Andrzejewska 1974, Breymeyer 1974, Wasilewska 1974).

Production of the above-ground parts of plants and the consumption by sheep were determined by measuring the biomass of plants under wire cages protecting the grass from sheep and on neighbouring areas grazed by sheep. The samples of plant material were collected every 4–6 weeks after which the cages were moved to other places. The consumption by sheep was determined as the cumulative value of differences between the green biomass in protected and grazed areas and the production was defined as the sum of sheep consumption, green plant biomass in the spring before grazing was started and the mean standing crop of this year dead mass (Andrzejewska 1974).

The production with moderate manuring (site *P*) was 554 g d.wt./m^2/season, and about two times higher (1057 g d.wt./m^2/season) with intense manuring (site *F*). The values obtained fit in with data for the production in mountains.

In the same plant community in Jaworki on experimental fields of the Institute of Land Reclamation and Cultivated Lands 400–495 g/m^2 of hay were obtained from a mown meadow (Kopeć and Kostuch 1966, Kostuch and Król 1966, Treter and Walewski 1971) while 678–753 g/m^2 were obtained when rational mineral fertilization was applied (Kostuch 1966, Treter and Walewski 1971).

In a similar meadow in Beskid Sądecki (*Festuca rubra* L. and *Agrostis vulgaris* With. dominant, i.e. the same as in the Pieniny pastures) located at the same level 421 g/m^2 and 765 g/m^2 were obtained respectively from unfertilized and fertilized (mineral fertilized) plots (Filipek and Skrijka 1973).

These values are similar to the ones we obtained taking into consideration that the yield of hay is only a part of the total production of the above-ground parts in which besides the yield the biomass of plants remaining in the field after the harvest (or grazing) and the mass of plants which die before the removal are taken into consideration. These parts which are not taken into consideration when only yields are considered amounted to 117 g dry mass in site *P*.

The consumption by sheep is a large percentage of green mass produced – over 80% of the above-ground production which is 206 g C/m^2/season. A considerable part of the consumed plant mass returns to the ecosystem in the form of faeces. On site *P* the amount of manure per year was 144 g C/m^2 or 70% of the plant mass consumed by the sheep.

The last value should not be taken as the digestibility index of the plant material by sheep. The distribution of manure in particular parts of pasture area is uneven and only the data on the distribution of the manure on the whole area could be used to calculate the degree of digestibility. This, however, was not included in the aims of the present work.

In one month duration experiments on the disappearance rate of manure (Olechowicz 1974) it was indicate that the weight of the manure at first decreases quickly for about 10 days and then the rate slows down (Olechowicz unpubl.). After 1 month 32% is mineralized. The experiment did not change the conditions of the habitat, it changed only one factor – the accessibility of manure for sheep trampling, which may tread down dungs, and contribute to their crumpling and mixing with the soil.

The results obtained in experiments allow an estimation of the rate of weight decrease of manure during the first 30 days of its presence in the pasture to be made. At this period the decrease in the weight of manure is known to be about 1/3 of the initial mass. However, the disappearance rate in successive weeks is not known.

An assumption was made that the decomposition rate in the pasture lasts for one more month that in the experiment and that all decomposition processes in the pasture cease at the end of October. This two month period of disappearance of manure was assumed on the basis of the statement that the rate of disappearance of manure depends on the amount of incoming manure (Kiełpiński, Karkoszka and Wiśniewska 1958). Thus the disappearance of manure in site *P* should be quicker than in site *F* where the whole area is covered by it. The disappearance of the main mass of manure from the area where sheep were penned-up was found to take 3–4 month (Jakubczyk 1974a). Thus we assumed on the basis of the experiments of Olechowicz (1971) and the data on the disappearance of manure from areas which had been used for penning-up sheep (Jakubczyk 1974a) that the disappearance of manure from the surface of the pasture takes longer than 1 and less than 3 months.

The process of disappearance of the manure was described by the equation:

$$N_t = N_o e^{\mu t}$$

where N_t – amount of manure at the end of the growing season, N_o – input per year, μ – coefficient of rate of disappearance, t – time (in days).

μ is a value calculated on the basis of experiments, it varies depending on the stage of aging of the manure.

On the basis of these assumptions it was calculated that 108 g C contained in the manure undergo mineralization and 36 g C pass into the soil.

As was observed in the experiments that coprophages – *Diptera* and *Scarabaeidae* play an important part in the processes of decomposition. In experiments in which isolation from these was used (by introducing steelon gauze covers) the disappearance rate was much slower. During one month only 13% instead of 32% underwent mineralization (Olechowicz 1974). The intensity of disappearance caused by microorganisms was evaluated on the basis of the difference of the rates of weight decrease of manure isolated and accessible to animals. This evaluation must be treated as only an approximation as it is based on the assumption that the activity of bacteria is the same in the presence and absence of coprophages while it was shown in a series of special experiments (Breymeyer, Jakubczyk and Olechowicz 1975) that the presence of animals changes microbial activity.

On the basis of the described one month long experiments (O l e c h o w i c z 1974) it was found that 73% of the total decrease in the weight of the manure was caused by respiration of organisms. 31.5% was due to respiration of coprophages and 41.5% to respiration of bacteria. The remaining 27% constitute insect production in the manure (Olechowicz unpubl.).

Another type of activity of organisms which is worth mentioning is the bringing of manure into the soil by adult *Scarabaeidae*. The intensity of this process was estimated as 18 g C/m^2/season (B r e y m e y e r 1974).

The decomposition rate of manure in the pasture is faster than that of dead plant material.

Tab. III. Rate of mineralization of manure and plant matter

Type of material	Rate of mineralization		Authors
	period (days)	decrease (mg/g)	
Manure:			
Bovine faeces	13	200	M a c D i a r m i d and W a t k i n (1972)
	30	310	
Sheep faeces in the habitat	13–15	200–210	
Lolio-Cynosuretum cristati	30	320	O l e c h o w i c z (1974)
Dead plant material in communities:			
Lolio-Cynosuretum cristati	30	190	A n d r z e j e w s k a (1974)
Spartina alterniflora	30	220	O d u m and de la C r u z (1967)
Serratuleto-Festucetum	30	135	
Glatiola officinalis-Carex praecox	30	135–150	J a r k l o v á (1972)
Glycerietum maxime	30	165	
Stellario-Deschampsietum	30	144	J a k u b c z y k (1971)
Arrhenatheretum elatoris	30	249–420	Ł o m n i c k i and B a n d o ł a (1967) J a k u b c z y k (1971)

The decomposition rate of various meadow plants and manure was compared on the basis of the literature (Tab. III). The greatest amount of data of this type come from forest ecosystems and concern a longer period, namely a year. However, as the experimental data obtained by us only include 1 month periods the rate of decay was only taken for such periods. Data for grassland ecosystems only are given.

The quality of the used material – its chemical content, degree of decay and climatic conditions – have a considerable effect on the decomposition rate. The differences in climatic conditions are hard to take into consideration as they are not always given in the papers. However, it may be assumed that the conditions of decay of plant material were not in general worse than the conditions of manure decomposition, and still the decomposition rate of dead plants was in general slower (Tab. III).

The rate of disappearance of plant material in an investigated pasture is also slower than the disappearance of manure. The rate of the former process was based on data on the decrease in the amount of dead plant matter in successive above-ground plant samples taken from April until the beginning of August, i.e. in the period during which no input of dead plant material in the field was observed (A n d r z e j e w s k a 1974).

In laboratory experiment performed by S a u e r b e c k (1968) and F l o a t e (1970) manure was found to decompose more slowly than plant material due to the higher content of easily decomposed sugars in plants than in manure.

However, in these experiments fresh plant material and not dead, partly leached plant material found in meadows was used. Moreover, there were no coprophages in the manure used for experiments and these, as has been shown by several workers, greatly accelerate the process of decomposition) B o r n e m i s s z a 1960, Olechowicz unpubl.).

Many data suggest that the presence of manure accelerates also the decomposition rate of dead plant matter.

The data of Z l o t i n (1971) which indicate that the addition of excrements of *Tortrix viridana* distinctly speeds up the leaves decomposition and that the excrements themselves decay completely within two months are of interest.

Another measure of the fast rate of manure decomposition may be the fact that the amount of manure remaining in the pasture is relatively very small in comparison with the amount coming in. The ratio of incoming to remaining manure is 36 : 1. This ratio indicates the rate of dispersion and fragmentation of manure rather than its mineralization but a similar index applied to the rate of disappearance of dead plant matter (ratio of plant mass dying during the year to the content of dead mass in the above-ground sward) is 1.6 : 1. The ratio of influx of dead plant matter into the soil to the content of detritus in the soil is much lower, 0.4 : 1. Thus the processes of plant decay taking place in the soil and above-ground are also slow in comparison to manure decomposition.

The above-mentioned data indicate that manure is not only decomposed faster than dead plant material but also that the influx of manure may accelerate the rate of plant decomposition and cause an intensification of mineralization processes in the soil.

The experiments have shown that animals play an important part in the decomposition processes of manure. The total respiratory activity is of the same order as that of bacteria, which is different than for the soil in which invertebrate metabolism constituted 21% of total heterotroph respiration.

3. PROCESSES OF CARBON TRANSFER IN AN INTENSIVELY MANURED ECOSYSTEM

The scheme of carbon flow in the area of pasture used for penning-up sheep in the previous year is much less complete than the previously discussed flow for site *P* as no measurements of belowground plant biomass were estimated.

The production of the above-ground parts of plants is, as was previously mentioned, approximately two times greater than in the pasture area not used for penning-up sheep (Fig. 2) (A n d r z e j e w s k a 1974) and about three times greater than in the area ungrazed (T r a c z y k and K o c h e v 1974, C z e r w i ń s k i et al. 1974). The consumption by sheep is, similarly as in the area not used for penning-up sheep, over 80% of the production of green parts of plants.

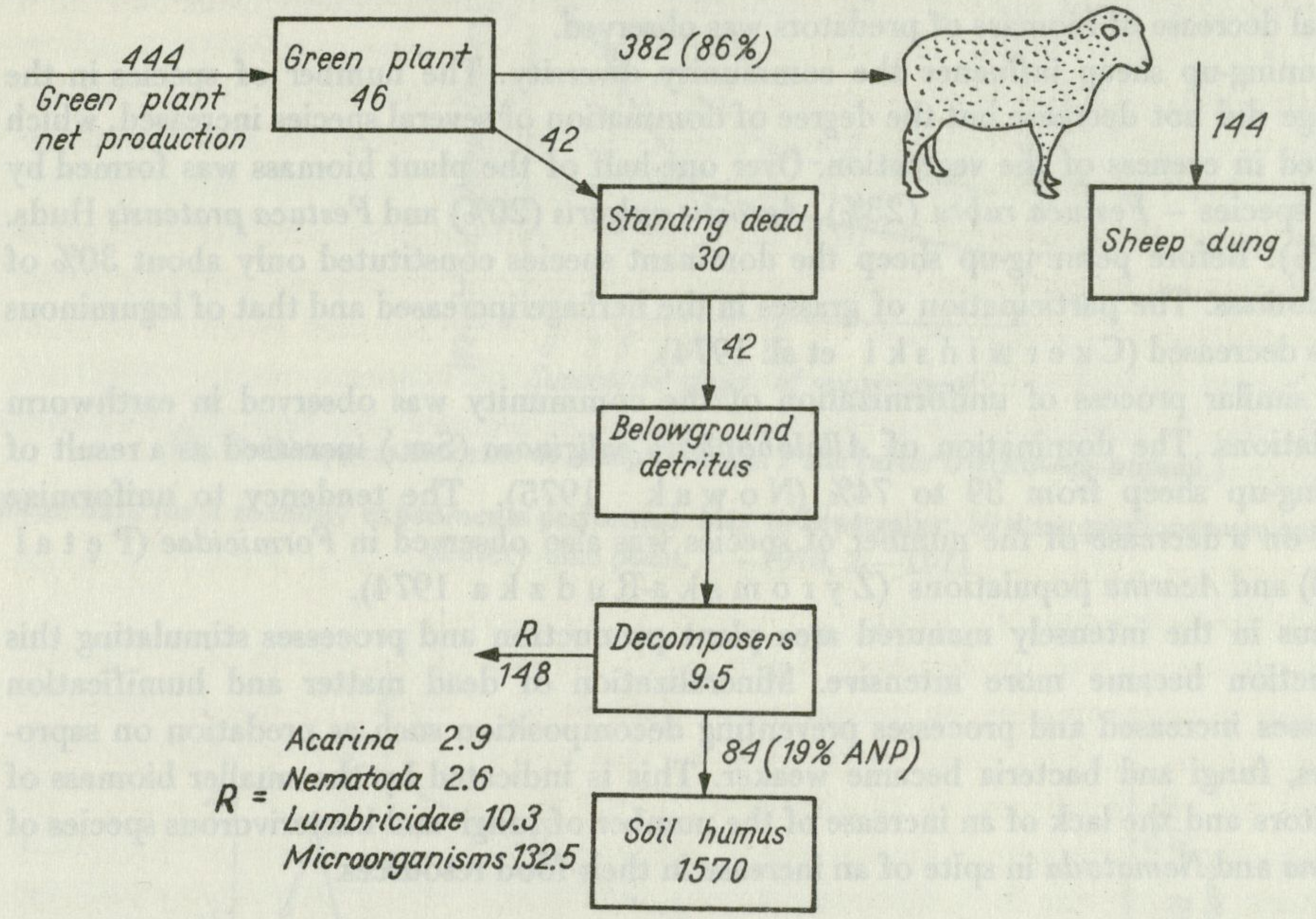

Fig. 2. Transfer of carbon in pasture ecosystem one year after penning-up sheep. Site *F*

For explanations see Figure 1. (Based on Andrzejewska 1974, Czerwiński, Jakubczyk and Nowak 1974, Czerwiński and Tatur 1974b, Jakubczyk unpubl., Nowak 1975. Wasilewska 1974, Żyromska-Rudzka unpubl.)

The activity of root-eating herbivores was more intense in this area. The biomass of herbivorous beetles of the family *Elateridae* increased four times (Tab. II).

The saprophages also were more active. The total respiratory activity of soil organisms increases four times in comparison with the previously described area. The biomass of earthworms increases to the same extent and that of bacteria twice. The proportion between input and decomposition of matter appears to be altered due to the considerable activity of saprophages. If we assume that the root system increases to the same extent as above-ground parts of plants as a result of penning-up sheep (what seems to be a reasonable assumption) the production and input of dead plant matter would be two times greater than before penning-up sheep while the respiratory processes increase 4 times as compare with site *P*. It is thus to be expected that detritus will not remain in the soil for a long time as happens in the poorly manured pasture.

In this intensively manured area the formation of humus was greatly increased. The intensity of this process measured as previously by the production of coprolites by earthworms increased about five times. This process was 18% of the above-ground plant production.

Thus in this rich habitat an increase in the biomass of consumers of plant material (both dead and living) was observed together with a decrease in the biomass of both soil and above-ground predators (Tab. II). Predator pressure on earthworm population tend to

be reduced (N o w a k 1975). Probably the reducing of predation is a general process and not only a process concerning earthworms in which alone it was studied, because the general decrease of biomass of predators was observed.

Penning-up sheep influence the community diversity. The number of species in the herbage did not decrease but the degree of domination of several species increased, which resulted in eveness of the vegetation. Over one-half of the plant biomass was formed by three species – *Festuca rubra* (23%), *Agrostis vulgaris* (20%) and *Festuca pratensis* Huds. (12.5%). Before penning-up sheep the dominant species constituted only about 30% of the biomass. The participation of grasses in the herbage increased and that of leguminous plants decreased (C z e r w i ń s k i et al. 1974).

A similar process of uniformization of the community was observed in earthworm populations. The domination of *Allolobophora caliginosa* (Sav.) increased as a result of penning-up sheep from 39 to 74% (N o w a k 1975). The tendency to uniformize based on a decrease of the number of species was also observed in *Formicidae* (P ę t a l 1974) and *Acarina* populations (Ż y r o m s k a-R u d z k a 1974).

Thus in the intensely manured area plant production and processes stimulating this production became more intensive. Mineralization of dead matter and humification processes increased and processes preventing decomposition such as predation on saprophages, fungi and bacteria became weaker. This is indicated by the smaller biomass of predators and the lack of an increase of the number of fungi- and bacterivorous species of *Acarina* and *Nematoda* in spite of an increase in their food resources.

4. SUCCESSION OF ORGANISMS CAUSED BY MANURING

Subsequent stages of succession taking place in the manure and soil during several subsequent months starting from the moment in which manure was introduced into the ecosystem, were observed.

Investigations on decomposition rate in general concern chemical or mass changes of material. In our investigations we also took into consideration changes in the world of living organisms.

The investigations of manure were performed on areas of the pasture where there was a small permanent input of manure (site *P*) and the soil investigations were mainly performed in the area which was used for penning-up sheep thus where one large influx of manure was implied. The range of the occurring processes is so large in the penning-up area that it is much easier to observe subsequent soil changes here. The character of the processes is probably similar in both examined areas. For the sake of easier comparison of manure with soil the data on the biomass of organisms are presented per 1 cm^3 substarte.

The decomposition rate of manure increases between the 3rd and 10th day and then tend to become much slower (Fig. 3) (Olechowicz unpubl.).

Manure during the first few hours of lying in the pasture is the domain of ammonifying bacteria. They constitute about one-half of the mass of manure. Their number gradually decreases from $3.54 \times 10^{10}/cm^3$ on the third day to $1.87 \times 10^{10}/cm^3$ manure after three weeks (Fig. 4).

Adult *Diptera* appear on the manure almost at once, but they do not feed on it, only lay eggs.

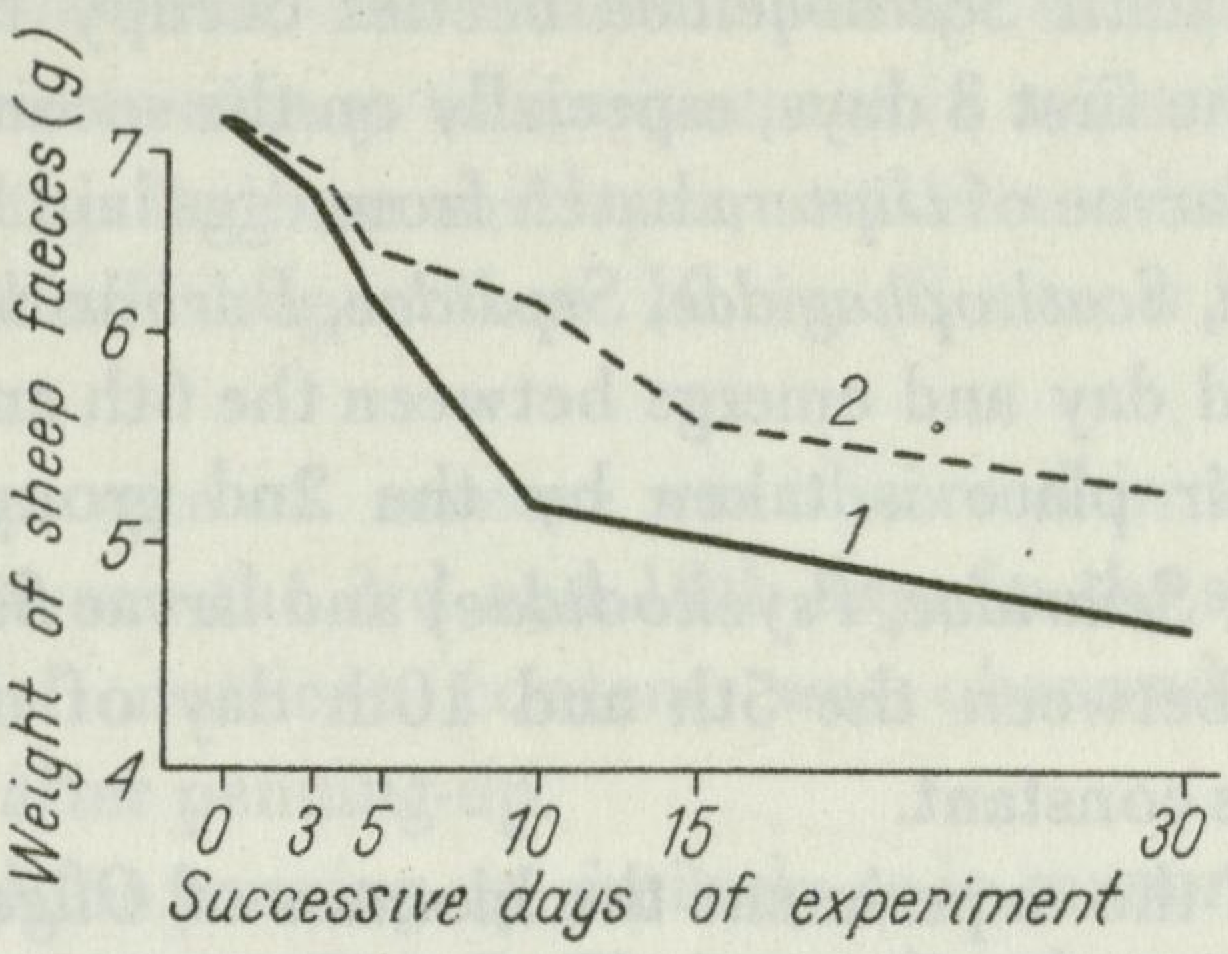

Fig. 3. Disappearance rate of sheep faeces in *P* site (after Olechowicz unpubl.)

Mean data for 5 monthly experiments performed May to September. 10 dung portions were analysed at every time point. *1* – 1970, *2* – 1971

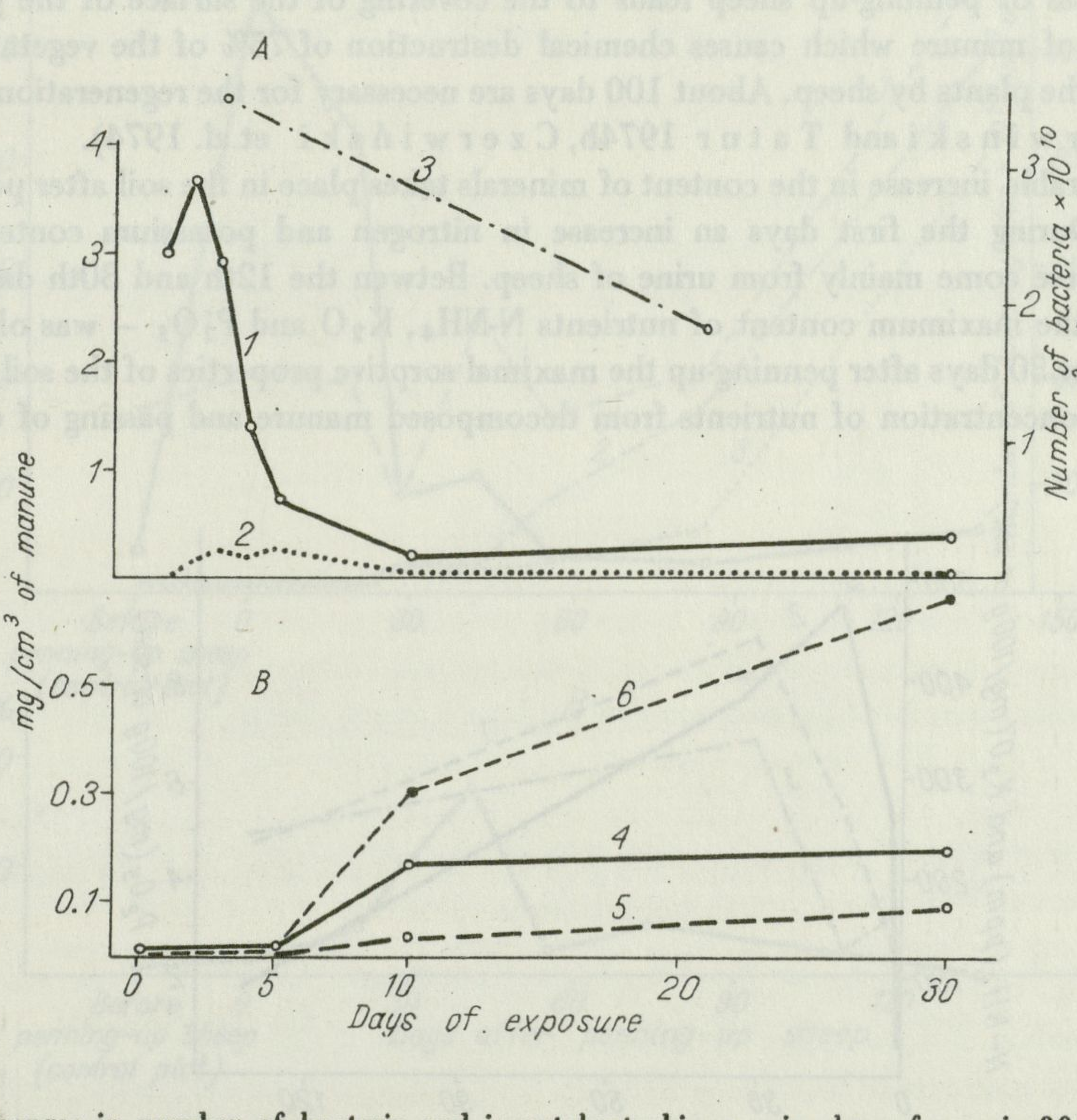

Fig. 4. Changes in number of bacteria and invertebrate biomass in sheep faeces in 30 days of dung exposure in *P* site. Data for 5 experiments carried out since May to September in 1970 (after J a k u b c z y k 1974a, O l e c h o w i c z 1974)

A **– organisms abundant mainly in first ten days of exposure,** ***B*** **– organisms abundant mainly between 10-th–30-th day of exposure,** ***1*** **–** ***Scarabaeidae*****,** ***2*** **–** ***Diptera*** **larvae (group I),** ***3*** **–** ***Bacteria*****,** ***4*** **–** ***Scarabaeidae*** **larvae,** ***5*** **–** ***Diptera*** **larvae (group II),** ***6*** **–** ***Lumbricidae + Enchytraeidae***

During the first day adult *Scarabaeidae* beetles occupy the manure. These are especially numerous during the first 3 days, especially on the second (Fig. 4).

During the first days larvae of *Diptera* hatch from eggs laid by members of the so-called 1st group (*Anthomyidae, Scathophagidae, Sepsidae, Borboridae*) which attain their maximum biomass on the 3rd day and emerge between the 6th and 10th day of the duration of their life cycle. Their place is taken by the 2nd group of *Diptera* larvae (*Chironomidae, Cecidomyidae, Sciaridae, Psychodidae*) and larvae *Scarabaeidae*. The biomass of these groups increases between the 5th and 10th day of the manure presence in the pasture and then remains constant.

In the last period of the experiment the biomass of *Oligochaeta – Lumbricidae* and *Echytraeidae* increases gradually; the maximum biomass of these animals is observed after 30 days (Fig. 4).

The average dry mass of the animals in the manure was 3.8 mg/cm^3 in 1970 and 1.57 mg/cm^3 in 1971. *Scarabaeidae* – adults and larvae – constituted 70% of the animal biomass (O l e c h o w i c z 1974).

The process of penning-up sheep leads to the covering of the surface of the pasture with a layer of manure which causes chemical destruction of 75% of the vegetation or trodding of the plants by sheep. About 100 days are necessary for the regeneration of the plants (C z e r w i n s k i and T a t u r 1974b, C z e r w i ń s k i et al. 1974).

A considerable increase in the content of minerals takes place in the soil after penning-up sheep. During the first days an increase in nitrogen and potassium content was observed. These come mainly from urine of sheep. Betwen the 12th and 30th day after penning up the maximum content of nutrients N-NH_4, K_2O and P_2O_5 – was observed (Fig. 5). After 30 days after penning-up the maximal sorptive properties of the soil due to progressive concentration of nutrients from decomposed manure and passing of organic

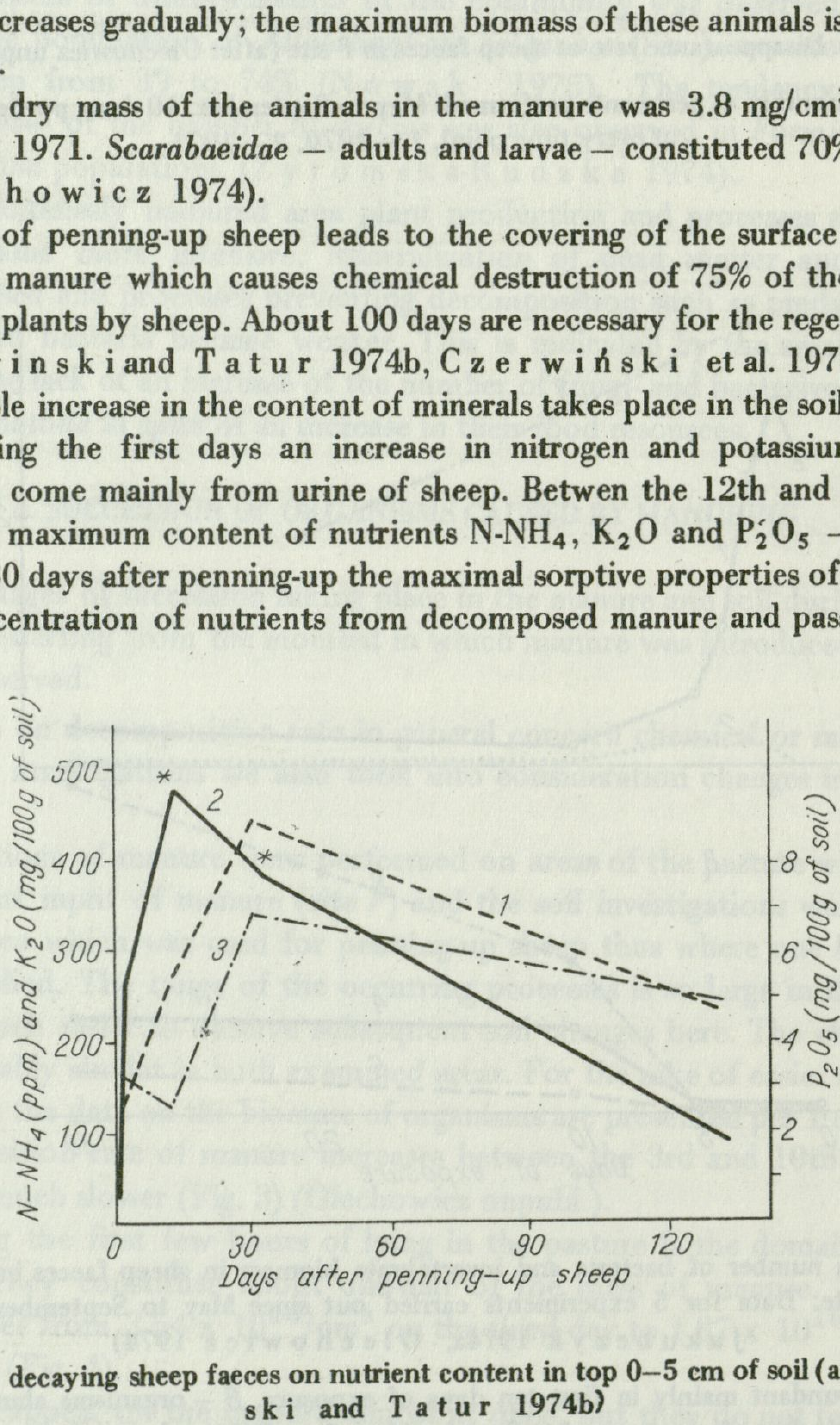

Fig. 5. Effect of decaying sheep faeces on nutrient content in top 0–5 cm of soil (after C z e r w i ń s k i and T a t u r 1974b)

1 – K_2O, *2* – NH_4, *3* – P_2O_5; *(asterisk) indicates the upper limit of sensitivity of the method substances into the soil was observed. The nutrient passage into particular layers of the soil is very differentiated. The tendency of an increase in mineral components was the most strongly marked in the top 0–2 cm soil layer, weaker and later in the next 2–5 cm layer and slight or not at all deeper than 10 cm (Czerwiński and Tatur 1974b).

The maximal disappearance rate of manure was observed in the period of maximal biomass of organisms, i.e. between the 3rd and 10th day. In the soil in the area used for penning-up sheep the maximal nutrient content was observed several days later, between the 12th and 30th day after penning-up.

In the soil of the area used for penning-up similarly as in manure mainly ammonifying bacteria are present in the first stages (Fig. 6). Their number decreases gradually and their

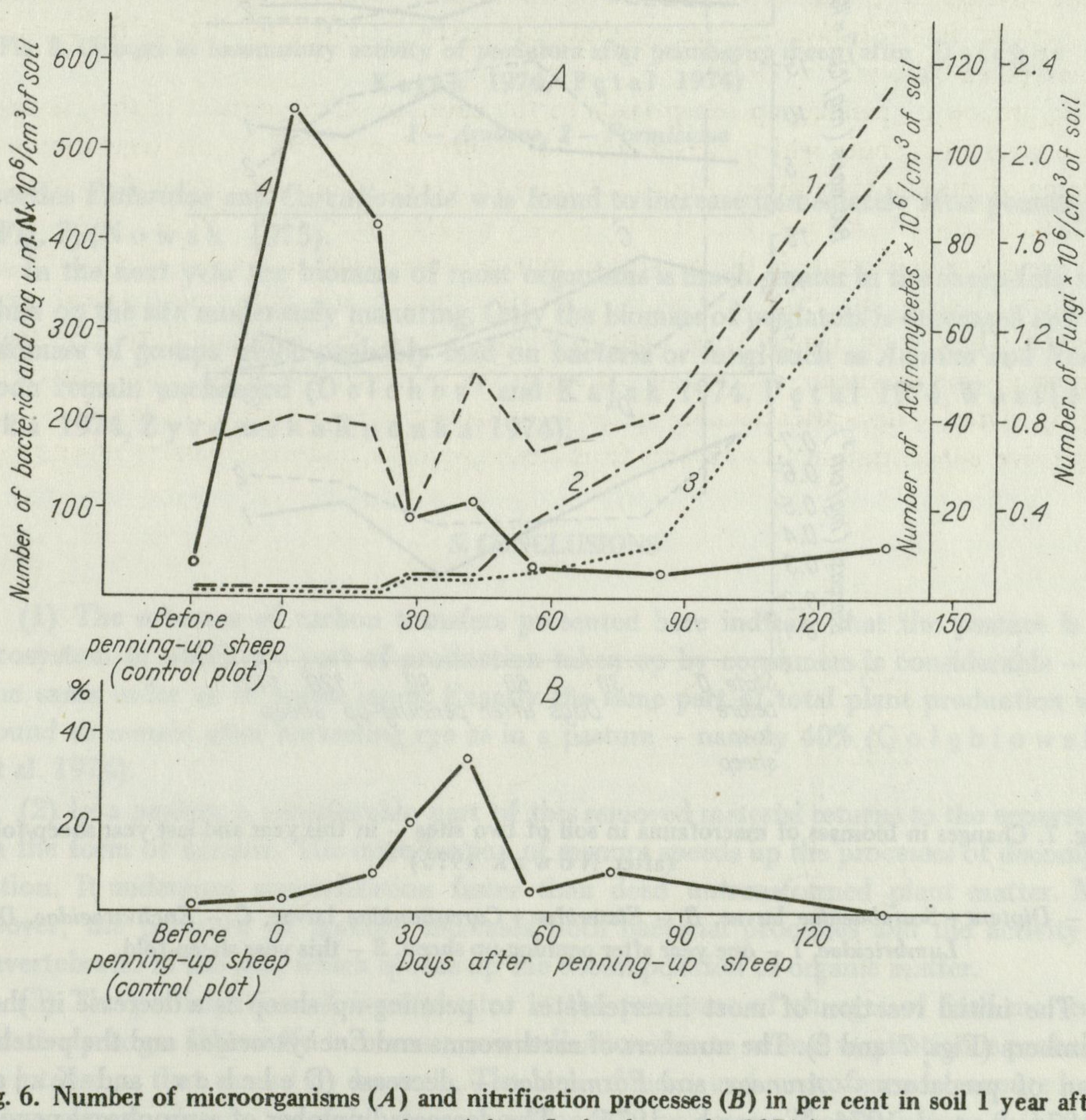

Fig. 6. Number of microorganisms (*A*) and nitrification processes (*B*) in per cent in soil 1 year after penning-up sheep (after Jakubczyk 1974a)

1 – *Fungi*, *2* – *Actinomycetes*, *3* – microorganisms utilizing mineral nitrogen, *4* – ammonifying bacteria maximum occurs during the first month after penning-up, with the greatest number present during the first days. During the second month nitrification processes become more intensive and subsequently again slower.

Other microorganisms – bacteria using mineral nitrogen, *Actinomycetes* and fungi gradually become more numerous in later succession stages. The maximum was observed 135 days after penning-up sheep (Fig. 6).

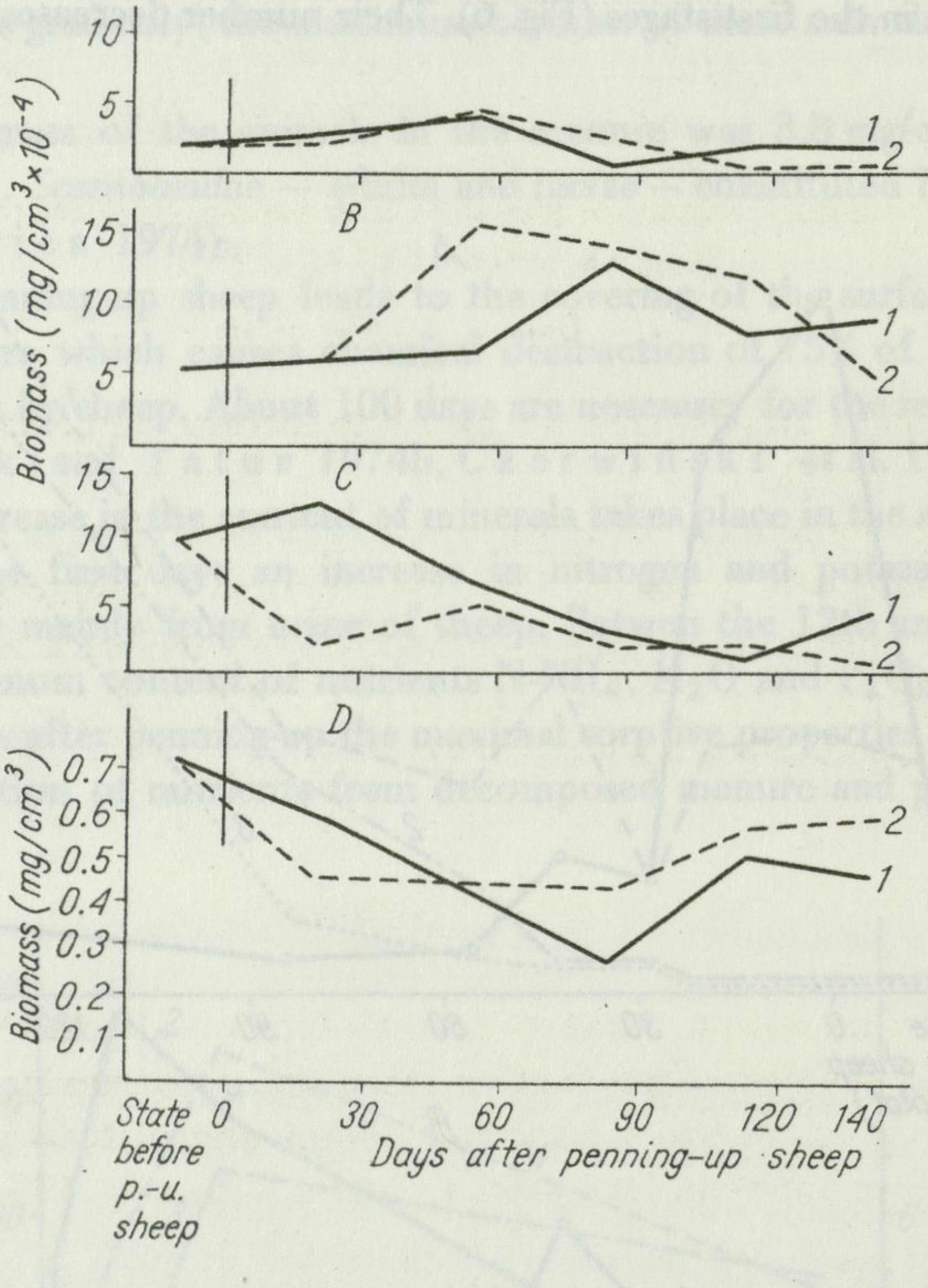

Fig. 7. Changes in biomass of macrofauna in soil of two sites – in this year and last year sheep-folds (after Nowak 1975)

A – *Diptera + Scarabaeidae* larvae, *B* – *Elateridae + Curculionidae* larvae, *C* – *Enchytraeidae*, *D* – *Lumbricidae*, *1* – one year after penning-up sheep, **2** – this year sheep-fold

The initial reaction of most invertebrates to penning-up sheep is a decrease in their numbers (Figs. 7 and 8). The numbers of earthworms and *Enchytraeidae* and the penetration of predators – *Araneae* and *Formicidae* – decrease (Delchev and Kajak 1974, Pętal 1974, Nowak 1975). The decreased number of saprophages persists for 2 months and the decreased penetration of predators for much longer. The number of larvae of coprophages – *Diptera* and *Scarabaeidae* – and the larvae of mainly herbivorous

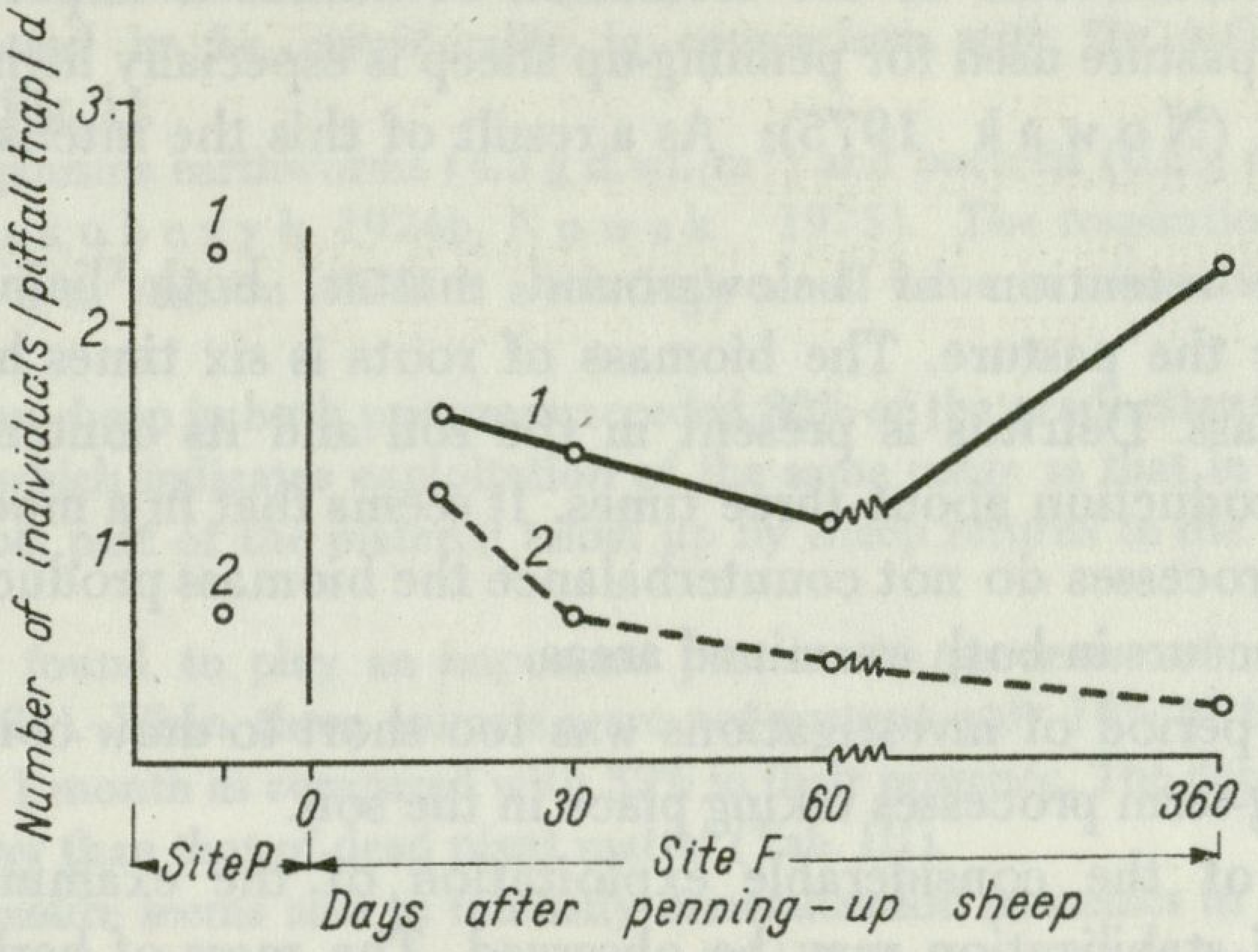

Fig. 8. Changes in locomotory activity of predators after penning-up sheep (after D e l c h e v and K a j a k 1974, P ę t a l 1974)

1 – Araneae, 2 – Formicidae

beetles *Elateridae* and *Curculionidae* was found to increase immediately after penning-up (Fig. 7) (N o w a k 1975).

In the next year the biomass of most organisms is much greater in the sheep-fold area than on the site moderately manuring. Only the biomass of predators is decreased and the biomass of groups which probably feed on bacteria or fungi such as *Acarina* and *Nematoda* remain unchanged (D e l c h e v and K a j a k 1974, P ę t a l 1974, W a s i l e w s k a 1974, Ż y r o m s k a-R u d z k a 1974).

5. CONCLUSIONS

(1) The schemes of carbon transfers presented here indicate that the pasture is an ecosystem in which the part of production taken up by consumers is considerable – of the same order as in arable lands. Exactly the same part of total plant production was found to remain after harvesting rye as in a pasture – namely 40% (G o ł ę b i o w s k a et al. 1974).

(2) In a pasture a considerable part of this removed material returns to the ecosystem in the form of manure. The introduction of manure speeds up the processes of decomposition. It undergoes mineralization faster than dead untransformed plant matter. Moreover, the presence of manure increases both bacterial processes and the activity of invertebrates in the soil, which speeds up the decomposition of organic matter.

(3) The participation of invertebrates in the processes of changes of dead matter is relatively large. Especially in manure mineralization due to animal respiration is probably as intense as that caused by bacteria. The lack of meso- and macrofauna in manure leads to an almost slower twofold decomposition rate processes. The respiratory activity of soil saprophages also is considerable in comparison with that of bacteria (the former is 27% of the latter).

The role of earthworms in the formation of humus is important. The biomass of earthworms in a pasture used for penning-up sheep is especially high, much higher than in mown meadows (N o w a k 1975). As a result of this the intensity of humification is especially high.

(4) The great retention of belowground matter, both liaing and dead, is also characteristic for the pasture. The biomass of roots is six times higher than the above--ground plant mass. Detritus is present in the soil and its content exceeds the underground plant production about three times. It seems that in a moderately manured area decomposition processes do not counterbalance the biomass production. Humus accumulation probably occurs in both examined areas.

However, the period of investigations was too short to draw conclusions on the direction of these long-term processes taking place in the soil.

(5) In spite of the considerable exploitation of the examined ecosystem several characteristics of stabilization may be observed. The mass of herbivorous invertebrates which are often pests of cultivated fields is small and stable.

After application of a large dose of manure the leaching of mineral components into the soil profile is small and is not intensive. Most nutrients stay in the top layer of soil (C z e r w i ń s k i and T a t u r 1974b).

The stability of this system is also indicated by the retention of organic matter in the soil.

One of the mechanisms stabilizing this system is the influx of coprolites into the soil. The chemical content of coprolites is almost constant in spite of differences in soil composition. The intensification of microbiological processes which takes place in coprolites is the strongest in poor habitats. Depending on the amount of organic matter and degree of decomposition in the soil different microbiological processes become more intensive in coprolites (C z e r w i ń s k i, J a k u b c z y k and N o w a k 1974).

(6) After intensive manuring several changes take place in the medium as a result of which many groups of organisms disappear and only species which can develop on manure remain. This change is the strongest and longest in the case of biomass of predators and on the simplification of the structure of the community. A rapid increase of saprophages also takes place. Mineralization and humification in the soil become more intense.

I would like to thank Dr. Teresa Wierzbowska and J. Józwik, M.Sc., for proposing the mathematical solution and for calculations concerning the amount of manure disappearing from the pasture during the year.

6. SUMMARY

The transfer of carbon in two pasture ecosystems – a pasture with moderate manuring (site *P* – manured with 360 g d.wt./m^2/ season in small daily doses) and an area used for penning-up sheep (site *F*) manured intensively for 3 days 540 g d.wt./m^2 and subsequently with daily doses as the previous ecosystem – were analysed. This moderate dose corresponds to approximately 90 kg N/ha/season.

The flow of carbon in two trophic chains – the detritus chain and the grazing chain – was examined. The data concerning the amount of carbon in the ecosystem and the rate of flow of carbon are given in Figures 1 and 2.

The detritus food chain was found to be based mainly on underground plant matter which in site *P*

exceeded the above-ground mass six times and the content of dead and living plant matter in the soil (537 g C/m²) was found to be considerable in comparison with the influx of dead material (120 g C/m²/season) (Fig. 1).

Among the soil organisms earthworms (4.5 g d.wt./m²) and bacteria (0.5 g d.wt./m²) dominate in respect to biomass (J a k u b c z y k 1974b, N o w a k 1975). The respiration of all soil organisms was estimated as 38 g C/m²/season which is a relatively small value in comparison with the influx of dead organic matter.

The consumption by sheep in both pastures exceeded 80% of the production of above-ground plant parts (Figs. 1 and 2) which indicates exploitation of the same range as that in grain cultivated fields. However, a considerable part of the material taken up by sheep returns to the ecosystem in the form of manure.

Coprophages were found to play an important part in the processes of manure decomposition (O l e c h o w i c z 1974). When these animals were not present only 16% of the manure underwent decomposition during 1 month as compared with 32% in their presence. The decomposition of manure in the pasture was faster than that of dead plant matter (Tab. III).

The presence of manure seems also to intensify mineralization processes in the soil. After intense manuring an increase in the biomass and as a result of this in the respiratory activity of soil organisms was observed (Tab. II). An increase of humification processes also takes place due to an increase in the production of coprolites by earthworms and increase of the number of bacteria involved in these processes. Each year approximately 4 times more C passes into the humus than in the moderately manured site (Figs. 1 and 2) (C z e r w i ń s k i et al. 1974).

The description of the succession in manure and soil after penning-up sheep is given (Figs. 6, 7 and 8) together with the parallel changes in the mineral content of the soil (Tab. I, Fig. 5). After applying intense manuring several changes take place, the number of several groups of organisms decreases considerably for 1–2 months and subsequently a rapid development of saprophages and herbivores takes place. The strongest and most persistent is the decrease of the biomass of predators and the eveness of the structure of the plant community and of several animal communities (*Formicidae, Lumbricidae, Acarina*).

7. POLISH SUMMARY (STRESZCZENIE)

W pracy porównany został przepływ węgla w dwu ekosystemach pastwiskowych – mianowicie na pastwisku o umiarkowanym nawożeniu (stanowisko *P* – 360 g suchej masy nawozu w sezonie, w stałych, codziennych dawkach) i na koszarze (stanowisko *F* – nawożone intensywnie w ciągu 3 dni ilością 540 g s. m. nawozu/m², a następnie zasilane codziennymi dawkami tak jak ekosystem poprzedni).

Rozpatrzono przepływ węgla w dwóch łańcuchach troficznych – w łańcuchu detrytusowym i łańcuchu spasania. Dane dotyczące ilości węgla w ekosystemie i tempa przepływu węgla podano na figurach 1 i 2.

Stwierdzono, że łańcuch detrytusowy bazuje głównie na podziemnej masie roślinnej, która na stanowisku *P* sześciokrotnie przewyższa masę nadziemną, oraz że zawartość w glebie żywych i martwych części roślin jest stosunkowo duża (537 g C/m²) w porównaniu z ilością dopływającego martwego materiału (120 g C/m²/sezon) (fig. 1).

Wśród organizmów glebowych pod względem biomasy dominują dżdżownice (4,5 g s.m./m²) i bakterie (0,5 g s.m./m²); (J a k u b c z y k 1974b, N o w a k 1975). Respiracja wszystkich organizmów glebowych została oceniona na 38 g C/m²/sezon, co jest wartością stosunkowo małą w porównaniu z ilością detrytusu dopływającego do gleby.

Konsumpcja owiec na obu pastwiskach przekraczała 80% produkcji nadziemnych części roślin (fig. 1 i 2), co oznacza eksploatację środowiska tego rzędu co w uprawach zbóż. Jednak znaczna część pobranego przez owce materiału wraca do ekosystemu w postaci nawozu (fig. 1).

Istotną rolę w procesach rozkładu nawozu odgrywają, jak stwierdzono, owady koprofagiczne (O l e c h o w i c z 1974). W warunkach izolacji od tych zwierząt rozkładało się w ciągu miesiąca tylko 16% wyłożonego nawozu, natomiast przy ich obecności w środowisku – 32%. Rozkład nawozu na pastwisku odbywał się szybciej niż rozkład martwego materiału roślinnego (tab. III).

Dopływ nawozu nasila, jak się wydaje, także procesy mineralizacji w glebie. Po intensywnym nawożeniu stwierdzono również znaczny wzrost biomasy, a co za tym idzie także nasilenie respiracji organizmów glebowych (tab. II). Następuje też wzmożenie procesów humifikacji. Powiększa się mianowicie znacznie produkcja koprolitów dżdżownic i związanych z nimi grup bakterii.

Rocznie przechodzi w próchnicę około czterokrotnie więcej C niż na stanowisku umiarkowanie nawożonym (fig. 1 i 2); (Czerwiński et al. 1974).

Podane zostały opisy sukcesji organizmów po koszarowaniu (fig. 6, 7, 8) oraz zachodzących równocześnie zmian w zawartości składników mineralnych w glebie (tab. I, fig. 5). Po zastosowaniu intensywnego nawożenia następuje w środowisku szereg zakłóceń, liczebność szeregu grup organizmów bardzo zmniejsza się na okres 1–2 miesięcy, po czym następuje gwałtowny wzrost liczebności zwierząt saprofagicznych i roślinożernych. Najsilniej i najdłużej to zakłócenie odbija się na zmniejszeniu biomasy drapieżców i uproszczeniu struktur zbiorowiska roślinnego oraz szeregu zespołów zwierzęcych (*Formicidae, Lumbricidae, Acarina*).

8. REFERENCES

1. Andrzejewska L. 1974 – Analysis of a sheep pasture ecosystem in the Pieniny mountains (the Carpathians). V. Herbivores and their effect on plant production – Ekol. pol. 22: 527–534.
2. Berthet P. 1964 – L'activitè des Oribatides (*Acari: Oribatei*) d'une Chenaie – Mém. Inst. r. Sci. nat. Belg. 152.
3. Bornemissza G. F. 1960 – Cold dung eating insects improve our pastures? – J. Aust. Inst. agric. Sci. 26: 54–56.
4. Breymeyer A. 1974 – Analysis of a sheep pasture ecosystem in the Pieniny mountains (the Carpathians). XI. The role of coprophagous beetles (*Coleoptera, Scarabaeidae*) in the utilization of sheep dung – Ekol. pol. 22: 617–634.
5. Breymeyer A., Jakubczyk H., Olechowicz E. 1975 – Influence of coprophagous arthropods on microorganisms in sheep feces – laboratory investigation – Bull. Acad. pol. Sci. Cl. II. Ser. Sci. biol. 23.
6. Czerwiński Z., Jakubczyk H., Nowak E. 1974 – Analysis of a sheep pasture ecosystem in the Pieniny mountains (the Carpathians). XII. The effect of earthworm on the pasture soil – Ekol. pol. 22: 635–650.
7. Czerwiński Z., Jakubczyk H., Tatur A., Traczyk T. 1974 – Analysis of a sheep pasture ecosystem in the Pieniny mountains (the Carpathians). VII. The effect of penning-up sheep on soil, microflora and vegetation – Ekol. pol. 22: 547–558.
8. Czerwiński Z., Kotowska J., Tatur A. 1974 – Analysis of a sheep pasture ecosystem in the Pieniny mountains (the Carpathians). I. Short geobotanical characteristics – Ekol. pol. 22: 475–486.
9. Czerwiński Z., Tatur A. 1974a – Analysis of a sheep pasture ecosystem in the Pieniny mountains (the Carpathians). II. The soil-geological conditions – Ekol. pol. 22: 487–504.
10. Czerwiński Z., Tatur A. 1974b – Analysis of a sheep pasture ecosystem in the Pieniny mountains (the Carpathians). VI. The effect of penning-up sheep on some chemical properties of soil – Ekol. pol. 22: 535–546.
11. Cummins K. W. 1967 – Calorific equivalents for studies in ecological energetics – Pymatuning Lab. of Ecology, Univ. of Pittsburgh, 52 pp.
12. Dahlman R. C., Kucera C. L. 1965 – Root productivity and turnover in native prairie – Ecology, 46: 84–89.
13. Delchev Kh., Kajak A. 1974 – Analysis of a sheep pasture ecosystem in the Pieniny mountains (the Carpathians). XVI. Effect of pasture management on the number and biomass of spiders (*Araneae*) in two climatic regions (the Pieniny and the Sredna Gora mountains) – Ekol. pol. 22: 693–710.
14. Filipek J., Skrijka P. 1973 – Rola azotu, fosforu i potasu w nawożeniu górskiej łąki kośnej w zależności of charakteru zbiorowiska roślinnego i warunków siedliskowych. II. Doświadczenia na łące typu kostrzewy czerwonej, mietlicy pospolitej i kostrzewy łąkowej – Acta agr. et silv. Ser. Agraria, 13: 19–31.

15. Floate M. S. J. 1970 – Decomposition of organic matter from hill soils and pastures. II. Comparative studies on the mineralization of carbon, nitrogen and phosphorus from plant materials and sheep faeces – Soil Biol. Biochem. 2: 173–185.
16. Gołębiowska J., Margowski Z., Ryszkowski L. (in press) – An attempt to estimate the energy and matter economy in the agrocenoses (In: Ecological effects of intensive agriculture. Ed. L. Ryszkowski) – PWN, Warszawa.
17. Jakubczyk H. 1971 – Decomposition rate of organic matter and microbiological activity (In: Productivity investigation of two types of meadows in the Vistula Valley) – Ekol. pol. 19: 121–128.
18. Jakubczyk H. 1974a – Analysis of a sheep pasture ecosystem in the Pieniny mountains (the Carpathians). VIII. Development of microflora in dung and in soil of a spring sheep-fold – Ekol. pol. 22: 559–568.
19. Jakubczyk H. 1974b – Analysis of a sheep pasture ecosystem in the Pieniny mountains (the Carpathians). IX. Decomposition processes and development of microflora in the soil – Ekol. pol. 22: 569–588.
20. Jankowska K. 1967 – Sezonowe zmiany roślinności i produkcja pierwotna netto w płacie łąki *Arrhenatheretum elatioris* – Studia Naturae, 1: 153–174.
21. Jarklová J. 1972 – Decomposition of dead plant matter in four alluvial communities (In: Ecosystem study on grassland biome in Czechoslovakia – PT – PP/IBP Report.) – 2: 65–70.
22. Jensen H. L. 1936 – Contributions to the microbiology of Australian soils – Proc. Linn. Soc. N. S. W. 41: 27–55.
23. Kiełpiński J., Karkoszka W., Wiśniewska St. 1958 – Badania nad koszarzeniem łąk i pastwisk górskich – Roczn. Nauk roln. F, 72: 1055–1086.
24. Klapp E. 1962 – Łąki i pastwiska – PWRiL, Warszawa, 600 pp.
25. Kopeć S., Kostuch R. 1966 – Kształtowanie się wilgotności gleb oraz plonów na pastwiskach górskich nawożonych i nienawożonych w zlewni Czarnej Wody koło Jaworek – Roczn. Nauk roln. D, 118: 135–160.
26. Kostuch R. 1966 – Użytki zielone zlewni Białej Wody – Roczn. Nauk roln. 118, 161–184.
27. Kostuch R., Król J. 1966 – Użytki zielone zlewni Czarnej Wody na tle stosunków fizjograficznych zlewni własnej oraz zlewni Białej Wody w Jaworkach – Roczn. Nauk roln. 118: 185–215.
28. Kostuch R., Kuc J. 1973 – Wpływ wysokości koszenia na plon i skład botaniczny górskich użytków zielonych – Wiad. Inst. Mel. Użyt. Ziel. 11: 103–121.
29. Kotańska M. 1970 – Morfologia i biomasa podziemnych organów roślin w zbiorowiskach łąkowych Ojcowskiego Parku Narodowego – Studia Naturae, A, 4: 1–108.
30. Kubicka H. 1973 – The evolution of CO_2 in two meadow communities – Ekol. pol. 21: 73–88.
31. Kucera C. L., Dahlman R. C., Koelling M. R. 1967 – Total net productivity and turnover on an energy basis for tallgrass prairie – Ecology, 48: 536–541.
32. Lewis J. K. 1971 – The Grassland biome: A synthesis of structure and function, 1970 (In: Preliminary analysis of structure and function in grasslands. Ed. N. R. French) – 317–387.
33. Luxton M., Thomas I. O. M. 1972 – Mites (In: Report of IBP/PT Theme 8 Meeting – Soil fauna and decomposition processes) – Louvin, 108–144.
34. Łomnicki A., Bandoła E. 1967 – Szybkość znikania martwych części roślin jako podstawa oceny produkcji pierwotnej netto ekosystemów lasu bukowego i łąki w Ojcowskim Parku Narodowym – Studia Naturae, 1: 19–24.
35. MacDiarmid B. N., Watkin B. R. 1972 – The cattle dung patch 2. Effect of a dung patch on the chemical status of the soil, and ammonia nitrogen losses from the patch – J. Br. Grassld Soc. 27: 43–48.
36. Nowak E. 1975 – Population density of earthworms and some elements of their production in several grassland environments – Ekol. pol. 23.
37. Odum E. P., de la Cruz A. A. 1967 – Particulate organic detritus in a Georgia salt marsh – estuarine ecosystem – Am. Assoc. Adv. Sci. Publ. 83: 383–388.
38. Olechowicz E. 1974 – Analysis of a sheep pasture ecosystem in the Pieniny mountains (the Carpathians). X. Sheep dung and the fauna colonizing it – Ekol. pol. 22: 589–616.

39. P ę t a l J. 1974 – Analysis of a sheep pasture ecosystem in the Pieniny mountains (the Carpathians). XV. The effect of pasture management on ant population – Ekol. pol. 22: 679–692.
40. P l e w c z y ń s k a-K u r a ś U. 1974 – Analysis of a sheep pasture ecosystem in the Pieniny mountains (the Carpathians). IV. Biomass of the upper and underground parts of plants and of organic detritus – Ekol. pol. 22: 517–526.
41. R e i c h l e D. E. (in press) – An advance in ecosystem study.
42. R e u s s J. O. 1971 – Decomposer and nitrogen cycling investigations in the grassland biome (In: Preliminary analysis of structure and function in grasslands. Ed. N. R. French) – 133–146.
43. S a u e r b e c k D. 1968 – Comparison of plant material and animal manure in relation to their decomposition in soil (In: Isotops and radiation in soil organic matter studies) – Vienna, 219–225.
44. S i m s P. L., S i n g h J. S. 1971 – Herbage dynamics and net primary production in certain ungrazed and grazed grasslands in North America (In: Preliminary analysis of structure and function in grasslands, Ed. N. R. French) – Fort Collins, 59–124.
45. S p e i d e l B., W e i s s A. 1971 – Primary production of a meadow (*Trisetum flavescentis hercynicum*) with different fertilizer treatments. Preliminary report (In: Integrated experimental ecology. Ed. H. Ellenberg) – Springer Verlag, New York; Heidelberg, Berlin, 61–67.
46. T e s a ř o v á M., G l o s e r J. 1972 – Soil respiration in a moist meadow plant community (In: Ecosystem study on grassland biome in Czechoslovakia – PT – PP/IBP Report) – 2: 91–93.
47. T r a c z y k T., K o c h e v Kh. 1974 – Analysis of a sheep pasture ecosystem in the Pieniny mountains (the Carpathians). III. Primary production of *Lolio-Cynosuretum* association – Ekol. pol. 22: 505–516.
48. T r e t e r K., W a l e w s k i R. 1971 – Wpływ terminu sprzętu pierwszego pokosu na wydajność łąki górskiej – Wiad. Inst. Mel. Użyt. Ziel. 10: 31–46.
49. W a s i l e w s k a L. 1974 – Analysis of a sheep pasture ecosystem in the Pieniny mountains (the Carpathians). XIII. Quantitative distrubution, respiratory metabolism and some suggestions on production of nematodes – Ekol. pol. 22: 651–668.
50. W i t k a m p M. 1971 – Forest soil microflora and mineral cycling (In: Productivity of forest ecosystems. Proceedings of the Brussels symposium 1969. Ed. Durigneau) – Unesco, Paris, 413–424.
51. W o o d T. G., L a w t o n J. H. 1973 – Experimental Studies on the Respiratory Rates of Mites (*Acari*) from Beech – Woodland Leaf Litter – Oecologia, 12: 169–191.
52. Z l o t i n R. I. 1971 – Invertebrate animals as a factor of the biological turnover (In: IV Collog. Intern. de la Faune du Sol. Dijon, 1970) – Paris, 455–462.
53. Ż y r o m s k a-R u d z k a H. 1974 – Analysis of a sheep pasture ecosystem in the Pieniny mountains (the Carpathians). XIV. The occurrence of oribatid mites, intermediate hosts of cestodes – Ekol. pol. 22: 669–678.

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