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PRODUCTIVITY INVESTIGATION OF TWO TYPES OF MEADOWS IN THE VISTULA VALLEY

XIII. SOME REGULARITIES IN STRUCTURE AND FUNCTION OF THE ECOSYSTEM

(Ekol. Pol. 19: 249–261). Analysis was made of some elements of the structure and functioning of three meadow ecosystems, on the basis of examination of soil, vegetation, invertebrate fauna and micro-organisms. It was found that invertebrate phytophages and decomposers occur numerously on fertile, more productive meadows. The decomposition rate of dead plant matter is correlated with the abundance of earthworms and bacteria dominating among the decomposers. Predatory forms are concentrated in the epigeion layer, where they find the most abundant food supply.

INTRODUCTION

Complex ecological studies were made of three meadow ecosystems situated in the Vistula Valley, at distances of 15 km from each other, and consequently subject to the same influences of the macroclimate. Fluctuations in maximum and minimum temperatures and atmospheric precipitation for this region were recorded by the local meteorological station (Fig. 1, Tab. I). Changes of

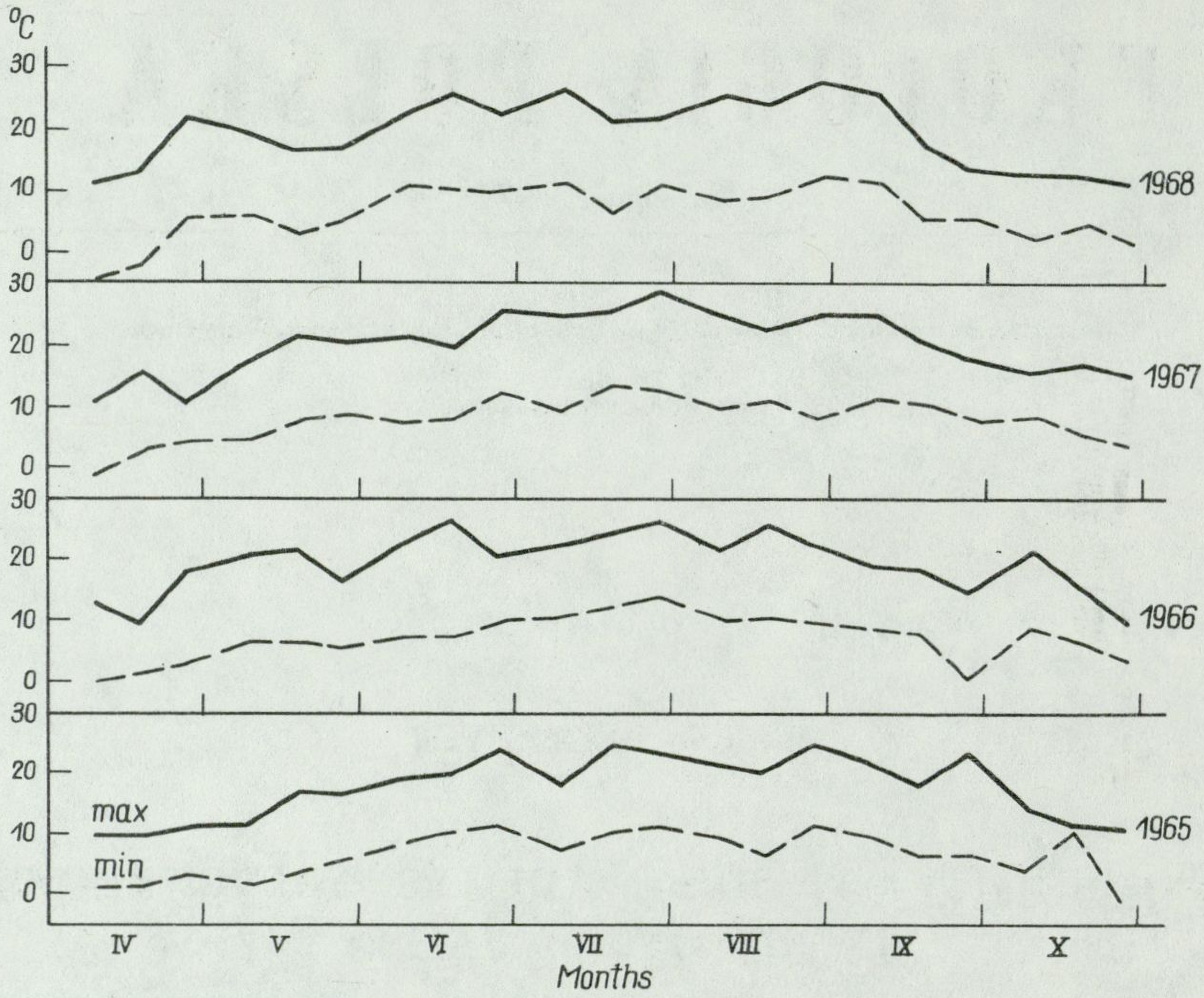

Fig. 1. Maximum and minimum air temperatures taken at the height of 2 m at the meteorological station at Dziekanów Leśny. The graph shows mean temperatures for ten days periods in the vegetation seasons of four consecutive years

Atmospheric precipitation during the four-year study period.
Meteorological Station, Grade III, at Dziekanów Leśny,
Nowy Dwór Mazowiecki administrative district, Vistula basin
(measurements in millimetres)

Tab. I

Months	Years			
	1965	1966	1967	1968
I	31.5	44.6	58.9	57.9
II	47.5	35.8	62.5	30.5
III	9.4	33.4	59.8	20.8
IV	49.6	30.0	71.4	23.5
V	101.4	65.6	57.5	46.8
VI	64.8	43.6	67.3	65.7
VII	86.7	68.1	50.7	59.4
VIII	75.9	61.4	44.9	14.5
IX	52.2	58.6	18.4	55.5
X	7.3	69.9	42.0	49.0
XI	43.2	81.5	32.3	41.1
XII	61.9	61.1	65.2	5.2
Total	631.4	654.6	630.9	469.9

ground water table measured on all the working stations in 1968 (Fig. 2) shows that the Strzeleckie Meadows (SM) are the wettest of the habitats examined, and the Kazuń Meadows area (symbol K I) the driest.

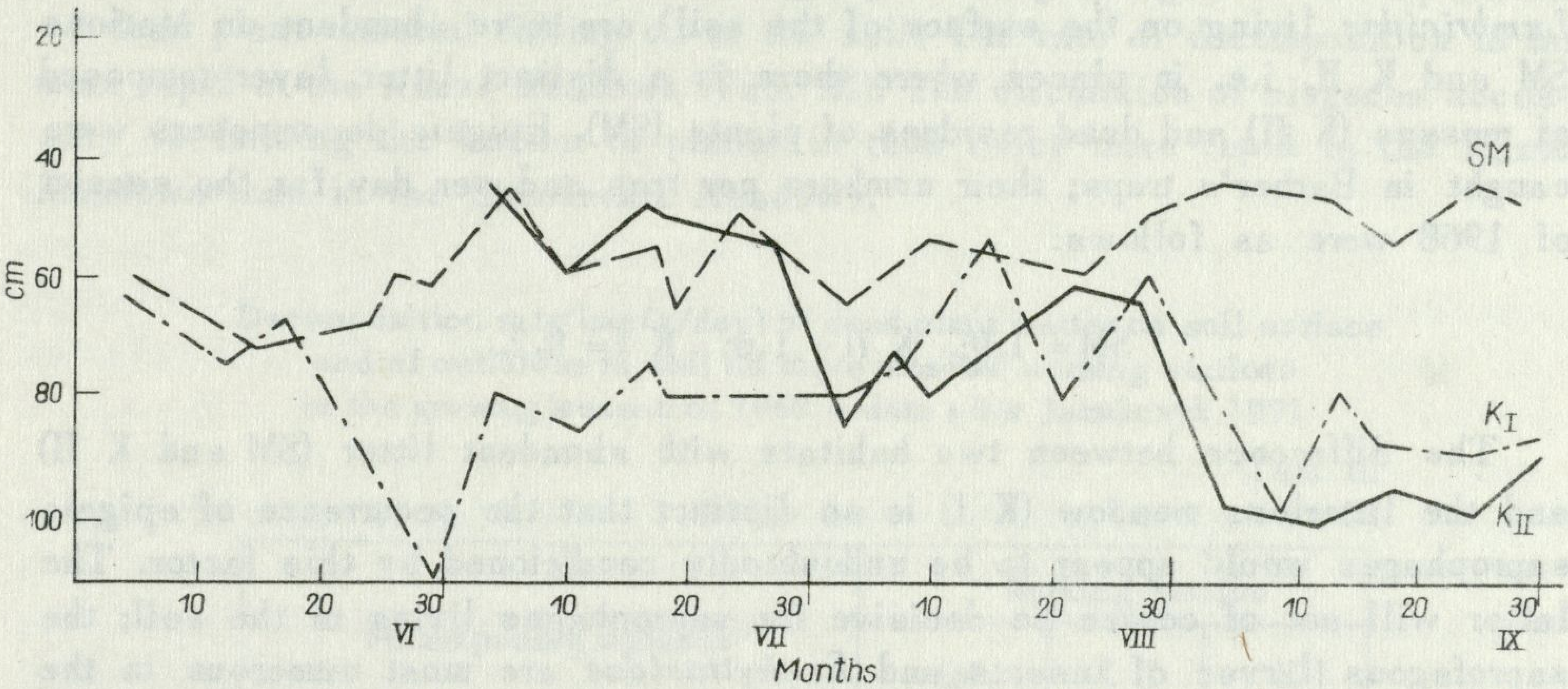

Fig. 2. Changes in ground water table (1968)

The Strzeleckie Meadows (SM) about 60 ha in area, situated within a wooded area, are surrounded by a dense wall of forest; these are meadows which have been included in the Kampinos National Park since 1965. The Kazuń Meadows (K I and K II) belong to the nearby farm; the only trees are the rows of willows growing along the drainage canals. The microclimates of the two meadow sets examined are different; in the Kazuń Meadows the higher vegetation is systematically removed (mown twice during the growing season), whereas in the nature reserve Strzeleckie Meadows the plant cover is left intact and is maintained throughout the whole season.

SOIL AND SOIL ORGANISMS

The soils of the study meadows differ greatly: the boggy soil of the Strzeleckie Meadows was formed from alluvial sands poor in nutrient components; the brown silts occurring on the Kazuń Meadows were formed from fertile alluvial deposits and constitute a natural, fertile meadow habitat (Czerwiński 1971).

The microbiological activity of these soils is appropriate to their fertility: the Kazuń Meadows are characterized by density of soil micro-organisms many times higher than the Strzeleckie Meadows (Jakubczyk 1971). Calculations made from Jakubczyk's data for 1968 on density of micro-otganisms ($\bar{N} \times 10^{11}$/ m^2/10 cm)[1] are:

[1] $\bar{N}$ – average number.

SM = 66.4; K II = 185.8; K I = 189.7.

The occurrence of the macrodecomposers of these habitats is more differentiated (Nowak 1971). All epigeic forms (*Isopoda*, *Diplopoda*, species of *Lumbricidae* living on the surface of the soil) are more abundant on stations SM and K II, i.e. in places where there is a distinct litter layer composed of mosses (K II) and dead residues of plants (SM). Epigeic decomposers were caught in Barber's traps; their numbers per trap and per day for the season of 1968 were as follows:

SM = 1.9; K II = 1.6; K I = 0.2.

The difference between two habitats with abundant litter (SM and K II) and the litterless meadow (K I) is so distinct that the occurrence of epigeic saprophages would appear to be undoubtedly conditioned by this factor. The latter will not of course be decisive for saprophages living in the soil; the saprofagous larvae of insects and *Enchytraeidae* are most numerous in the Strzeleckie Meadows (Tab. II). The far lower and very similar level of occurrence of these groups in the Kazuń Meadows suggests that this is due to some important factor which, by comparison with the Strzeleckie Meadows, is decisive in the Kazuń Meadows. This factor probably consists of the hydrological and soil conditions, very similar in the two Kazuń Meadows and differing in SM.

Numbers ($\overline{N}$/m^2/15 cm) of saprophagous larvae of insects and *Enchytraeidae* on three working stations in the growing season 1968

Tab. II

Group	Working station		
	SM	K II	K I
Saprophagous larvae of insects	49.3	4.6	4.0
Enchytraeidae	137.0	48.0	45.5

Earthworms, which dominate among macrodecomposers, differ in size on the working stations; comparison of their biomasses ($\overline{B}$ in gd.w./m^2/15 cm)[2] on these stations is as follows:

SM = 5.3; K II = 11.9; K I = 7.0.

[2] $\overline{B}$ – average biomass.

The lowest biomass of earthworms is therefore found in the Strzeleckie Meadows; this is a direction of variation compatible with the changes in numbers of microorganisms which are least abundant in the Strzeleckie Meadows.

The result of the activity of all groups of saprophages is decomposition of dead plant material falling on to the soil. The rate of decomposition is far more rapid in the Kazuń Meadows (Tab. III). The circulation of biogenes necessary to forming the bodies of plants is thus twice more rapid in the Kazuń Meadows than in the Strzeleckie Meadows.

Decomposition rate (mg/g/day) of dead plant matter on soil surface and of cellulose in soil on three meadow working stations in the growing/season of 1968 – data after Jakubczyk 1971

Tab. III

Decomposing material	Working station		
	SM	K II	K I
Dead plant matter	4.8	8.3	14.0
Cellulose	15.2	27.0	27.0

It would appear that these data should be treated as comparative and not absolute. The decompostion rate of dead plant matter in particular may increase during the experiment due 1) to the grass being laid out in the meadow in nylon net bags, in which a microclimate favourable to the development of microflora is created; 2) to care being taken to ensure that the bags lay closely adhering to the soil from which litter had been cleared, which undoubtedly improved conditions for development of microflora. Under natural conditions the dead plant matter falling to the soil is retained on the litter, where part of it dries up and becomes inaccessible of microflora.

Among the organisms responsible for the decomposition of organic matter on the working stations only earthworms and micro-organisms occur in minimum numbers on the Strzeleckie Meadows i.e. indicate the direction of variation similar to that found for decomposition rate of organic matter. This is not of course evidence that only these two groups play a part in the decomposition of organic matter, although it is probably they which are the most effective. It would appear possible that in SM, where macrosaprophages occur relatively abundantly, decomposition processes do not reach the final stage; they are initiated by intensively active macrodecomposers, but not continued correspondingly intensively by micro-organisms. Consequently we observe a far lower rate of decomposition of plant matter and cellulose in SM, and also consequently, despite the fact that accumulation of plant residue was not found on SM, there is retention of this kind of organic matter in a very considerable proportion as for a meadow habitat.

PRIMARY PRODUCTION

Traczyk (1971) gives the following values of annual production of the above ground parts of plants in these meadows in g d.w./m^2:

SM = 476; K II = 588; K I = 564.

Plant production of cultivated meadows is thus higher than the production of the nature reserve meadows, and if vascular plants only are taken into consideration, is several times higher (SM = 196 g, K II = 585 g, K I = 564 g).

About 90% of the plant matter produced in the Kazuń Meadows is collected by man; after two mowings only 50–60 g of dry plant mass remain on the square meter of the meadow. This amount is introduced into circulation in the ecosystem as dead plant matter (of course plus the matter taken during the season from plants by phytophages and introduced into circulation in the form of their bodies and faeces). In the Strzeleckie Meadows, on the other hand, the whole of the yearly crop (less the activity of phytophages) is returned to the ecosystem in the form of organic fall. According to Traczyk's data (1971) during the period of maximum development of the meadow herb layer at the height of the season, the mass of dead vegetation in SM is 240 g d.w./m^2, which forms over 30% of the whole biomass recorded on this working station at this time (the analogical values for K II – 62 g d.w./m^2 – 13%, and for K I – 91 g d.w./m^2 – 18%). At the beginning of the growing season ten times more dead than live mass is found on the Strzeleckie Meadows; up to midsummer these proportions shift in favour of live mass, but never proceed as far as complete disappearance of organic fall, as is the case in the Kazuń meadows. As a result SM are constantly covered by a far thicker layer of plant matter; since, however, accumulation of plant fall was not found it must be considered that despite the considerable retention of this form of organic matter the constant rate of its input and decomposition is maintained.

PHYTOPHAGES

Large phytophagous invertebrates probably play an unimportant part in the meadow ecosystems discussed. Although deer and elk, which are under protection in the reserve, are encountered in the Strzeleckie Meadows, and hares cause some damage in the cultivated meadows K I and K II, in both cases the effect is sporadic and probably plays an unimportant part here. In autumn a part of the surface of the meadows is destroyed by wild boar in their search for food. The number of boar visiting the meadows has been estimated and it will soon be possible to assess the extent of the areas rooted up by these animals.

Numbers of invertebrate phytophages on three working stations in the growing season of 1968

Tab. IV

Group	Working station		
	SM	K II	K I
Orthoptera $\bar{N}/m^2$	3.3	3.9	7.7
Homoptera $\bar{N}/m^2$	16.0	46.0	22.0
Diptera imagines Np/m^2 *	157.0	296.0	–
Phytophagous insect larvae $\bar{N}/m^2/15$ cm	4.2	16.0	31.2

* Np/m^2 – number of insect emerging hatching from 1 m^2 of meadow during season.

Rodents periodically occur on the meadows examined in fairly large numbers: their numbers and the destruction they cause to plants are being assessed at the present time.

Invertebrate phytophages occur constantly on these meadows in large numbers; the most numerous are representatives of *Orthoptera*, *Homoptera-Auchenorrhyncha* and *Diptera* (Tab. IV). There are distinctly larger numbers of the two main groups of phytophages (*Orthoptera*, *Homoptera*) in both the cultivated meadows. The some direction of variation is found when comparison is made of the number of imagines of phytophagous dipterans on these meadows (Olechowicz – verbal communication) and the density of phytophagous insect larvae in the soil (Nowak 1971).

More abundant occurrence of phytophages in the cultivated meadows is thus repeated several times in relation to the several different groups. It would thus appear an undoubted fact that cultivation and mowing of meadows create better conditions – probably primarily food conditions – for phytophages; the continuous regrowth of grass means that there is a constant supply of juicy, young blades which form the food of these animals. The second cause reducing the numbers of phytophages in the Strzeleckie Meadows is their intensive reduction by predators. The data given by Kajak and Olechowicz (1970) show that web spiders reduce from 25% (1968) to 40% (1967) of all flies emerging in the Strzeleckie Meadows during the growing season; there are periods (the reproduction period of spiders) when reduction reaches as much as 90% of the number of flies emerged. In the Kazuń Meadows, where the number of web spiders is far lower (Kajak, Breymeyer, Pętal 1971) the reduction of phytophages by these arthropods is correspondingly lower. A similar situation in relation to *Homoptera-Auchenorrhyncha* was found by Andrzejewska (1971). Despite the greater production of progeny the average numbers of these phytophages is lower in the Strzeleckie Meadows;

this is due to predators feeding on them intensively. In the Kazuń Meadows the lower production, but even smaller reduction of *Homoptera* results in far higher average numbers.

Destruction of grass by phytophagous invertebrates in the study meadows was estimated by several methods. The experimental method used by Andrzejewska and Wójcik (1971) consisting in exterminating all invertebrates gives very interesting but fairly variable results; maximum increase in crop on areas free of fauna is as much as 40% of plant mass in relation to control areas, where invertebrates existed under density conditions normal for the given meadow. It would, however, appear that as the effect on the soil of the poisons used and the organisms killed by them is unknown, these results must be treated with reserve. It is not known to what extent the more rapid increase of plant mass is due to elimination of phytophages from the areas treated with the poisons.

Destruction* caused by dominating groups of invertebrate phytophages on working stations

Tab. V

Group	Destruction of grass	SM	K II	K I
Orthoptera	g d.w./m²/season	23.8	28.0	48.3
	% P_p**	5.0	4.8	8.6
Homoptera	g d.w./m²/season	1.7	4.8	2.3
	% P_p	0.4	0.8	0.4
Total	g d.w./m²/season	25.5	32.8	50.6
	% P_p	5.4	5.6	9.0

*Calculation on basis of studies by Andrzejewska 1967, Andrzejewska, Wójcik 1970.

** P_p – primary production.

Destruction caused in the meadow by *Orthoptera* and *Homoptera-Auchenorryncha* was examined by means of laboratory and field experiments (Andrzejewska 1967, Andrzejewska, Wójcik 1970). Using one of the species of *Homoptera-Auchenorrhyncha* (*Cicadella viridis* L.), which occurs in dominating numbers, as an example, it was found that of all the grass losses caused by *Cicadella viridis* 70% is due to consumption, and 30% to destruction caused during feeding. *Orthoptera* cause far greater destruction; the amount of grass destroyed during feeding exceeds by six times, and even in the case of high grasses, ten times, the amount of grass eaten by these insects[3].

[3] Data given after Andrzejewska 1967, Andrzejewska, Wójcik 1970.

Losses in primary production caused by these two dominating groups of phytophagous invertebrates do not exceed 10% (Tab. V). This figure would undoubtedly increase considerably if we added to it estimated consumption, and in particular destruction caused by rodents; this is the third important group of herbiovores in the study habitats.

PREDATORS

The comparative material at our disposal refers to several groups of predatory invertebrates: predatory ants and flies, epigeic spiders and spiders living on grasses, and also predatory soil macrofauna (Tab. VI). The most abundant occurrence of predators is therefore recorded in the reserve meadow SM. It is difficult to give the factors conditioning this occurrence of all the groups discussed, although it is possible to do so for some of them. For epigeic spiders, and for some insect's larvae (*Carabidae*, *Staphylinidae*, *Tipulidae*)

Numbers and biomasses (mg d.w.) of invertebrate predators on three stations

Tab. VI

Group		SM	K II	K I
Predatory ants	$\bar{N}/m^2$	142.0	46.4	132.9
	$\bar{B}^*/m^2$	71.0	23.0	66.5
Epigeic spiders	$\bar{N}/m^2$	45.3	10.0	14.2
	$\bar{B}/m^2$	175.0	25.0	55.0
Web spiders	$\bar{N}/m^2$	52.0	4.4	0.6
	$\bar{B}/m^2$	78.3	5.2	1.3
Predatory flies (imagines)**	$\bar{N}_p/m^2$/season	54.9	20.0	
	$\bar{B}/m^2$/season	122.1	75.3	
Predatory larvae of beetles	$\bar{N}/m^2$	5.9	6.0	5.3

* $\bar{B}$ – mean biomass.
** Unpublished data, Olechowicz.

the presence of the litter layer is important. For ants the water level is of considerable importance (high in SM and K II) and on the other hand in SM the absence of agricultural cultivation, which destroys ant nests. Web spiders are conditioned very drastically by the presence (SM) or absence (K I, K II) of protruding plant stalks on which they can suspend their webs for trapping insects (Kajak 1971). Thus in relation to many groups the most important causes conditioning their occurrence and production would appear to be habitat factors, such as the general stability of the reserve ecosystem and abundant litter layer, rendering this habitat similar to a forest and creating a favourable microclimate on the surface of the soil; on the other hand continual agricultural operations destroying the natural structure of the habitat, absence of mosses and layers of dead plants on the cultivated meadows. It is difficult to say how important trophic factors are in conditioning the occurrence of predators. The abundance of invertebrates which can form the potential prey of predators is fairly similar on all the meadows examined and would probably be sufficient for the requirements of the latter. It would therefore appear that the potential food capacity of the cultivated meadows (K I, K II) in relation to predators is greater than that actually used; the development of the trophic network is not fully realized, primarily on account of the constantly repeated agricultural operations which destroy the habitat (cf. Kajak, Breymeyer, Pętal 1971). In the Strzeleckie Meadows the long-term development of the undisturbed ecosystem leads to growth of the trophic network and occupation of the maximum number of ecological niches. The abundance and variety of invertebrate predators can form a good indicator of the growth of the trophic structure; in the Strzeleckie Meadows the food chains conduct energy through three, and even four consumers-predators (Pętal, Breymeyer 1969). Cases of insects eating each other within one group of predators (epigeic spiders) are frequently found (Breymeyer 1967), which means that the energy stream is divided into bands which, as it were, "diverge" from the mainstream of the energy flow and return some part of transmitted energy to the preceding link in the food chain or, perhaps, form their own closed circulation.

Correlation of the numbers of predators with abundance of food was found in relation to their distribution in space – it is similar in all the study habitat; the soil surface is most densely occupied, the share of predators in this stratum differs from 26 (K I) to 54% (SM), whereas in herb stratum from 0 to 22% and in the soil from 0.2 to 3.2%. Such great density of predators in the epigeion is due to the fact that the great majority of the insects in meadow habitats pass through some stages of their development in the soil and during their vertical migrations connected with metamorphosis form an easy prey for predators (Kajak, Breymeyer, Pętal 1971). Olechowicz (1971) states that in 1968–1473 insects emerged from 1 m^2 of the Strzeleckie Meadows, and 1227 insects from an analogical area in K II. Almost all of them can form the prey of these above predators.

GENERAL REMARKS

The amounts of live and dead plant matter differ in the ecosystems examined. In the Strzeleckie Meadows the whole[4] of the green mass

[4] We assume that all the estimates of primary production given by us also include the activities of phytophages which have, as it were, taken place previously.

produced (470 g/m²) dies and passes into the pool of dead matter. In the two Kazuń Meadows, on the other hand, from about 600 g/m² of P_p (primary production) not much more than the 60 g/m² recorded in autumn passes into the pool of dead matter.

The above comparison shows that in the two types of ecosystems which we examined SM belongs to the "detritus", and K I and K II to the "grazed" type. The consumers of live and dead plant matter are phytophages and saprophages (Tab. VII).

Biomasses ($\bar{B}$ in g d.w./m²) of dominating groups of phytophages and saprophages on working stations

Tab. VII

	SM	K II, K I
Orthoptera, Homoptera	0.14	0.20– 0.31
Lumbricidae, Bacteria	8.5	17.3 –24.1

The abundance of green mass in the cultivated meadows thus has its counterpart in the subsequent links in the food chain – animals feeding on green mass are also numerous on these working stations. The case is different with the detritus food chain. Despite the very great abundance of dead plant mass in SM it is not followed by relative abundance of decomposers. Thus in the Strzeleckie Meadows the energy retained in dead matter is passed on slowly to the further links in the food chain, it may be said with a degree of delay. Some habitat factors probably render it inaccessible to detritus-eating organisms.

Invertebrate predators occur most abundantly in the nature reserve Strzeleckie Meadows: this can be seen quite clearly when comparison is made of biomasses ($\bar{B}$ in g d.w./m²) of the two most numerous groups of predators (spiders, ants) on the working stations:

$$SM = 0.32; \quad K\,II,\ K\,I = 0.05–0.12.$$

We suggest that the cause of the smaller number of predators in cultivated meadows consists of habitat factors. It is also possible that the predators examined by us are particularly sensitive to agricultural operations; it may be that other forms, e.g. parasites more closely connected with the host's body than with the external habitat, regulate population density in the biocenoses of cultivated meadows.

Use has been made in this study of some unpublished information obtained from members of our research group, chiefly from Drs. L. Andrzejewska, A. Kajak, E. Nowak, E. Olechowicz and T. Traczyk. These colleagues, and also the other members of the group, made contributions to the discussions which were of invaluable assistance in a study aiming at interpreting different results. My thanks are due to them for the information they supplied and for the interest they took and the time they kindly devoted to discussions.

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BADANIA PRODUKTYWNOŚCI DWU TYPÓW ŁĄK W DOLINIE WISŁY

XIII. NIEKTÓRE PRAWIDŁOWOŚCI BUDOWY I FUNKCJONOWANIA EKOSYSTEMU

Streszczenie

Analizowano kompleksowe badania ekologiczne trzech ekosystemów łąkowych; były to pospolite w Polsce łąki z rzędów *Molinietalia* i *Arenatheretalia* położone w dolinie Wisły w okolicy Warszawy. Dwie z badanych łąk należą do gospodarstwa rolnego Kazuń i są w normalnym użytkowaniu (koszone dwa razy w sezonie), trzecia łąka tzw. Łąka Strzelecka położona jest w Kampinoskim Parku Narodowym i w związku z tym nie używana przez człowieka (oznaczenia łąk użytkowanych – K I i K II, łąki w Parku Narodowym – SM). Charakterystykę środowisk oparto na pomiarach zmian poziomu wody gruntowej, wilgotności gleby i temperatur maksymalnych i minimalnych powietrza i gleby. Wielkość produkcji roślinnej skorelowana jest na badanych łąkach z żyznością gleby i aktywnością destrucentów; na łąkach o wyższej aktywności mikrobiologicznej gleby i większej biomasie makrosaprofagów stwierdzono szybsze tempo rozkładu martwej materii organicznej oraz większą produkcję pierwotną. W ślad za obfitością świeżej, stale odrastającej trawy na tych łąkach idzie większa liczebność roślinożerców bezkręgowych. W wyniku eksperymentów laboratoryjnych i polowych oszacowano efekt działania tych roślinożerców na roślinność; straty wynoszą ok. 20% produkcji rocznej. Byłyby one o wiele wyższe gdyby nie działalność drapieżników bezkręgowych, które szczególnie intensywnie redukują roślinożerce na łące położonej w Parku Narodowym. Niektóre rodziny muchówek redukowane są przez pająki sieciowe w 80–90% (w stosunku do liczebności populacji dojrzałej); redukcja w stosunku do wszystkich muchówek wynosi ok. 30% liczby imagines.

Ogólnie stwierdzono, że biorąc pod uwagę losy materii organicznej wytwarzanej na obu typach łąk (uprawiane i nie użytkowane) można zaliczyć pierwsze z nich do ekosystemów spasanych, drugie do detritusowych. Obfitość zielonej masy na łąkach uprawianych znajduje swój odpowiednik w następnych członach łańcucha pokarmowego – zwierzęta pasące się zieloną masą są na tych stanowiskach także liczne. Inaczej jest w przypadku detritusowego łańcucha pokarmowego. Mimo ogromnej obfitości martwej masy roślinnej na SM nie postępuje za nią względna obfitość detritofagów. Na Łąkach Strzeleckich energia retencjonowana w martwej materii jest więc przejmowana przez dalsze ogniwa wolno, można powiedzieć, z opóźnieniem. Prawdopodobnie jakieś czynniki środowiskowe czynią ją niedostępną dla organizmów detritusożernych.

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