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THE INFLUENCE OF *ACRIDOIDEA* ON THE PRIMARY PRODUCTION OF A MEADOW (FIELD EXPERIMENT)

(Ekol. Pol. 18: 89–109) This is an attempt at assessing the influence of phytophagous grasshoppers (*Acridoidea*) on the primary production of a meadow. Grounds for assessment were as follows: 1) losses in plant biomass due to feeding by grasshoppers, defined in a field experiment; 2) dynamics of density and biomass of grasshoppers determined in the meadow; 3) daily consumption by grasshoppers examined under laboratory conditions.

Losses in plant biomass were found to depend on the density of the insects, the time at which they fed and the properties of the plant cover and species of plants on which they feed. The density of insects has a particularly great effect on extent of losses in plant biomass caused not by the insects feeding, but by destruction of the plants.

Contents

I. INTRODUCTION

Various anthors give various assessments of the role of phytophagous insects as competitors with man in reducing primary production. Some of them consider that losses due to feeding by phytophagous insects are very low, and so omit them from further considerations. They assess the effects of feeding, and thus the value of losses of plant mass, on the basis of the amount consumed by the phytophages examined (Howard and Odum 1957, Smalley 1960, Wiegert 1964). This is not, however, always justifiable. Frequently variations in plant production values due to feeding by phytophagous insects differ considerably from the amount of food consumed by these insects. Trojan (1967) found that moderate feeding by phytophages may not reduce production of those parts of plants which are of economic importance, as may be the case when the Colorado beetle feeds on potato plants. According to Varley (1967) the green mass of plants may even be increased, if the phytophage feeding on the plant delays its flowering and prolongs the period of leaf production.

Cases have been described in which the losses in plant production caused by phytophages feeding on plants are many times greater than the food actually consumed by the insects. In such instances phytophages present in the habitat, even with moderate density, may be responsible for considerable losses in primary production. Attention is drawn to the important role of phytophagous invertebrates in reducing the primary production of the forest herb layer by Rafes, Dienesman, Perel (1964), and of timber – by Varley and Gradwell (1962), Varley (1967) and to their important influence on the primary production of pastureland – by Tischler (1955), of cereals – Nuorteva (1962), of grass – Andrzejewska (1961, 1967), Macfadyen (1967). These authors take into consideration the amount of plant mass eaten by the phytophage and destroyed during feeding. Losses caused in this way to primary production vary from a small to a very high percentage.

It is not always possible to make an unequivocal evaluation of the part played by phytophages in the biocenosis, since this depends on many factors. The species of phytophages and its feeding habits are essential. Also the density of phytophages is always of primary importance. Likewise the role of phytophages depends to a great extent on such factors as: which parts of the plant are destroyed, to what degree and during which stage of development the plant is usually damaged, and finally how the damage caused by insects affects its normal development.

The purpose of the experiment described in this paper was to obtain data for assessing the losses in green plant mass in a meadow caused by the feeding of *Acridoidea*. These insects, along with *Auchenorrhyncha*, form one of the dominating groups of phytophagous insects living in the meadow habitat we examined.

II. HABITAT

The experiments were made in the Strzeleckie Meadows situated in the north-east part of the Kampinos Forest, in two plant associations: *Stellario-Deschampsietum* Freitag 1959 and *Caricetum elatae* W. Koch 1926. A phytosociological and ecological description of these associations is given in the study by Traczyk (1966).

These associations differ considerably in the structure of the vegetation and amount of primary production, and thus they create different living conditions for the animals as well as different experimental conditions.

Vascular plants of the *Stellario-Deschampsietum* association (working station *D*) grow up from a dense moss cushion, which leaves no ground bare. *Deschampsia caespitosa* P.B., the most common of the vascular plant species growing in this meadow in respect of both constancy of occurrence in different patches of the meadow and in respect of the degree to which it covers the area occupied by the association, grows in compact tussocks about 20 cm in diameter. Other species forming less compact tussocks, or growing from long stolons, and also species growing singly, are distributed very irregularly between the tussocks. Although the main mass of vegetation of this meadow is formed by low sedge and grasses, the role of dicotyledonous plants in the association is not unimportant. Various species occur there constantly, attaining a high degree of coverage and producing a large amount of green organic matter. This increases the mosaic character of the meadow. If this association is analysed by means of the large square method (20–100 m^2), as in phytosociological studies, the habitat turns out to be outstandingly uniform (see Tab. VII in the study by Traczyk 1966). If, however, it is necessary to use a smaller area in experimental studies (they measured 0.64 m^2 in ours) then one may notice how varied the vegetation is.

In the reedswamp association, *Caricetum elatae*, (working station *Mc*) the main component, *Carex hudsoni* Bennet, grows in large, compact tussocks set on high stocks rising above the small depressions separating them. The diameter of the tussocks in the habitat we examined was from 60–80 cm. Most often there is no other plant in the dense mass of several hundred or several thousand shoots of *C. hudsoni*. The small depressions are occupied by other species of sedge, chiefly *C. vesicaria* L. with a small admixture of *C. rostrata* Stokes. Other components of the associations, chiefly large plants of order

Phragmitetalia, although they occur with considerable constancy in large-area phytosociological records, are scantily scattered and play an unimportant part in our study area. Mosses are also of little importance in this association. The typical variant of the *Caricetum elatae* association evaluated on the basis of Traczyk's (1966) 20 m records (see his Tab. II – records 7–29) appears to be almost as uniform as the previous association. When the association is divided up – as under our experimental conditions – into small areas, it splits into completely separate elements of the mosaic; it either includes the tussock, omitting the depressions, or the depression only without the tussock. Each of the areas included, however, shows no lesser uniformity of vegetation than cultivated fields sown with one variety of plant.

In respect of primary production, and in particular the primary production of vascular plants, these associations differ considerably. According to the studies made at the same time by Traczyk (1968), the annual production of vascular plants in the *Stellario-Deschampsietum* was 173 g per 1 m² of meadow. Plants used as food by grasshoppers form 67–68% of this and three species of plants taken for assessment in the present experiment – 48.5%. We estimated the primary production of vascular plants in the *Caricetum elatae* association as amounting to about 550–600 g per 1 m². 90% of this is formed by the large sedges used as food by grasshoppers.

III. METHODS

The influence of consumption by grasshoppers on the vegetation of the meadow was assessed by means of an experiment. Small parts of the area of the meadow (squares of 0.8 × 0.8 m) were covered by a dense net stretched over a cubic metal frame. After frightening away or removing all the insects from under the nets all the grasshoppers caught from the meadow surrounding the isolators were placed under them. Consequently the species composition of grasshoppers and quantitative relations among grasshopper species under the nets and in the surrounding habitat were similar. The weights of grasshoppers caught in the meadow during this period and used for the experiment were less than 60 mg. The density of these insects under the isolators was several times greater than in the surrounding meadow. The initial density of the insects introduced was: 100, 300 and 500 insects per 0.64 m². Control nets without insects were set up for purposes of comparison. The physical habitat conditions for the insects under the isolators were almost the same as those in the meadow, as the thin net of the isolator, permitting free passage of air, altered the microclimate of the area enclosed in the isolator to a minimum degree only. Nets containing insects were set up on July 2nd 1965 on station *Mc*, and on July 27th 1965 on station *D*, and were not taken down until the autumn disappearance of insects.

Analysis of the attractiveness as food to the grasshoppers showed that monocotyledonous plants almost exclusively form the food of these insects in the habitat examined. That is why the leaves of these plants were used for assessment of losses in plant mass. Grasshoppers prefer feeding on leaves growing vertically or almost vertically, a far smaller percentage feeding on leaves in a horizontal position. This agrees with the observations made by Kaufmann (1965). Of the dicotyledonous plants only *Plantago lanceolata* L., which has elongate leaves pointing upwards, was subject to a certain degree of biting. This species was, however very scantily scattered in the vegetation of a meadow of the *Stellario-Deschampsietum* type and in *Caricetum elatae* it did not occur at all.

In the experiments made in the *Caricetum elatae* association, we examined losses of green mass in two species of sedge – *Carex hudsoni* and *C. vesicaria*, two outstanding dominants of this association, which jointly yielded the greater part of the plant biomass produced there (over 90%). In experiments in the *Stellario-Deschampsietum* association we analysed losses of mass of two sedges – *C. panicea* and *C. fusca*, and of one grass – *Deschampsia caespitosa*, jointly forming about 2/3 of the biomass of the vascular plants of the association (Traczyk 1968).

Losses caused by grasshoppers feeding were determined twice: approximately after the third and after the sixth week from the time of introducing the insects under the net. 50 shoots of selected species of plants eaten by grasshoppers were taken from under each isolator. They were cut off close to the ground, the first time along one diagonal of the square covered by net, and the next time along the second diagonal. This gave a far better check on the degree of damage to these plants under the whole isolator than did taking them from a small area within the isolator.

Loss in primary production caused by grasshoppers was calculated from the difference between the biomass of 50 plants taken from isolators containing insects, and the biomass of 50 plants from the control isolators. The values obtained were in turn converted to unit of area, taking into account the exact data on primary production of the meadow. In particular, we used production of the examined species, set out in Traczyk's study on the primary production of the *Stellario-Deschampsietum* association in the Strzeleckie Meadows (Traczyk 1968), and the authors' own estimates of primary production of the *Caricetum elatae* association.

In addition to losses in the biomass of grass under the isolators, the daily consumption by grasshoppers and their density in the surrounding meadow were determined. Daily consumption by grasshoppers, i.e. the amount of grass eaten daily by one insect in different stages of development, was calculated in the laboratory. Several grasshoppers of a known weight were placed in jars. The bottom of those jars was covered with damp sand (to prevent over-drying of the insects). The grasshoppers were weighed every few days to discover any variations in their biomass. Every day, after carefully collecting all the remains of grass from the previous day, the insects were given a weighed portion of fresh grass. The daily food requirements of the grasshoppers in each jar was calculated from the differences in weight between the grass fed to the insects and the remains which were collected. Finally, the daily consumption of grass by all the grasshoppers was evaluated per individual and per unit of body weight (in mg).

To eliminate differences in water contents in the grass fed to the insects and the uneaten remains which they left, all calculations of daily consumption were made on dry mass of grass. As it was, of course, impossible to feed the insects on dried grass, at the same time as their food was prepared, from 5 to 10 similar portions of grass were dried in order to determine their dry mass contents, assuming that the water content in the grass given to the grasshoppers was the same.

Density of the grasshoppers in the surrounding meadow was estimated on the basis of samples taken with a biocenometr. 10 randomly chosen squares of meadow, measuring 0.5 × 0.5 m, were covered with nets stretched on metal frames forming boxlike isolators. All the grasshoppers were removed from under the net by means of a sucking apparatus. Sampling was carried out once a week, from the start of the growing season, in the spring to the autumn disappearance of grasshoppers, i.e. from May to October. The insects caught were dried and weighed, and on this basis the variations in average biomass of one grasshopper and the biomass of the whole population and its variations over the season were calculated.

IV. RESULTS OF EXPERIMENTS

1. Amount of grass consumed by a grasshopper during its lifetime

Results of laboratory cultures indicate that daily consumption by grasshoppers depends on the size of the individual, its condition and physiological state. Larval individuals weighing from 10–20 mg eat on an average 0.67 mg of fresh grass mass per 1 mg of mass of individual; large individuals weighing from 20–60 mg – eat 0.4 mg. As they mature, together with increase in the grasshopper's body weight the daily consumption per unit of body weight of larvae and males decreases and is on an average 0.2 mg of fresh grass mass per 1 mg of individual (Fig. 1).

In adult females during the egg-laying period (about two weeks) the amount of food consumed gradually increases. Towards the end of a female's life, after the eggs have been laid, the daily consumption per unit of biomass is

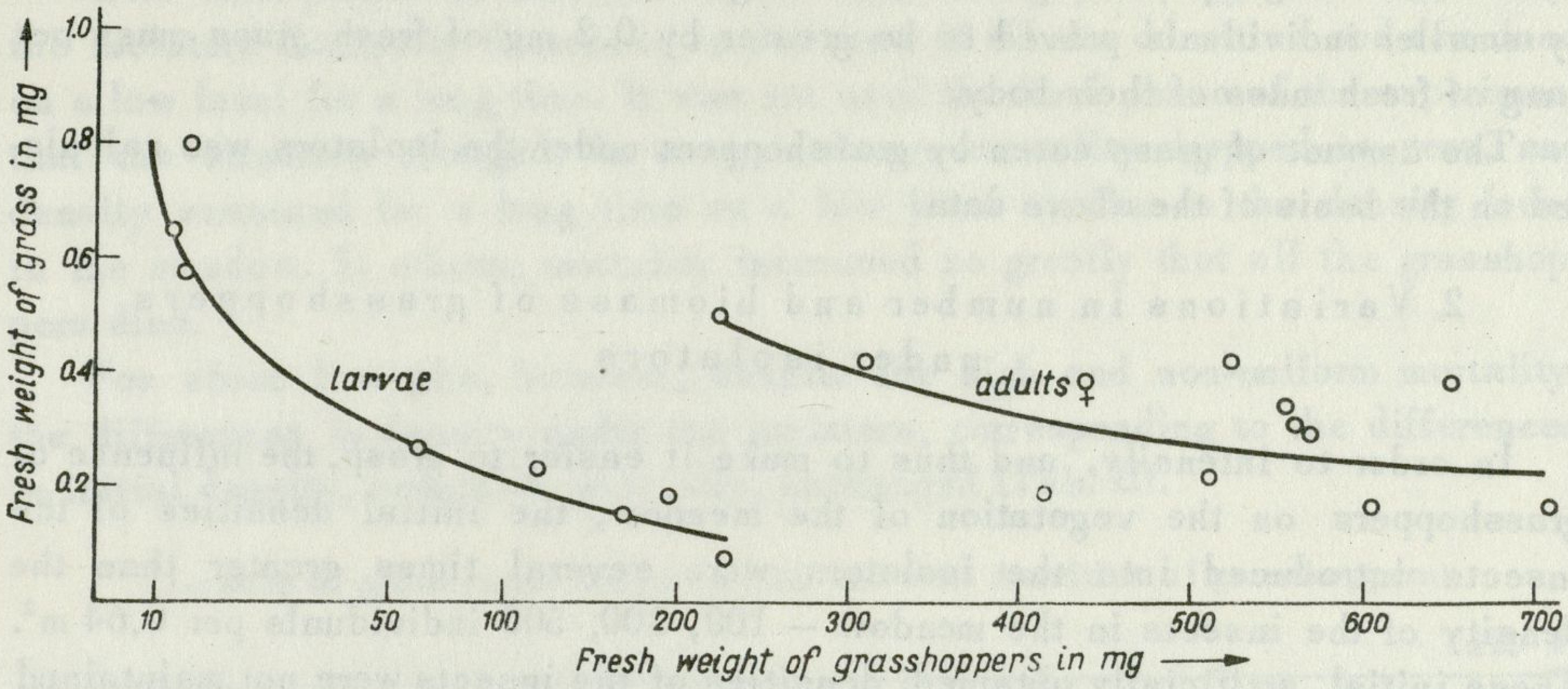

Fig. 1. Daily consumption of grass by one grasshopper depending on its biomass (in mg), Each point is average of 20 measurements

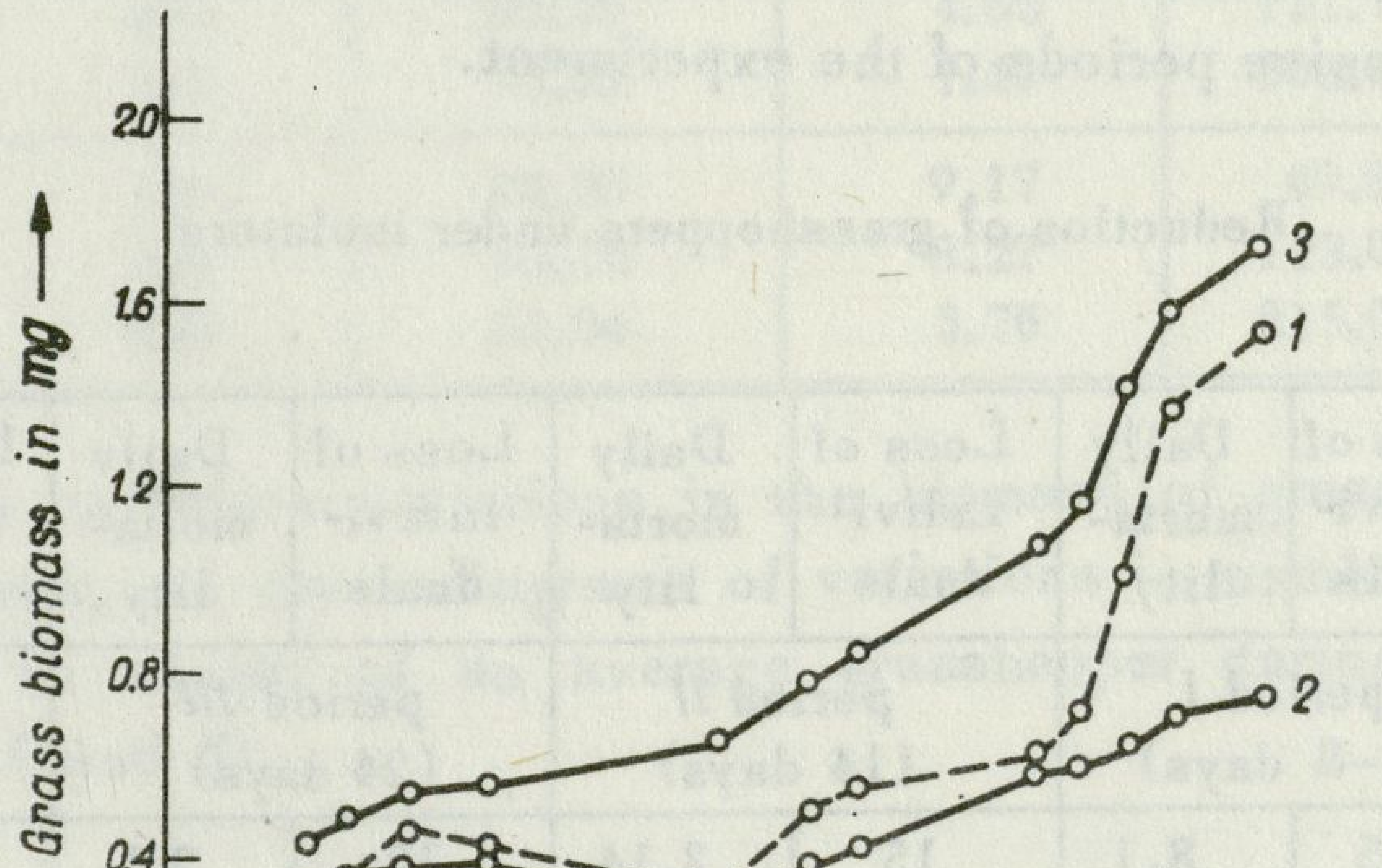

Fig. 2. Variations in time of daily consumption in adult female grasshoppers. Each point is average from 10 individuals

1 – *Chorthippus dorsatus*, 2 and 3 – *Mecostethus grossus*

exceptionally great, similar to the daily consumption of the youngest larval stage (Fig. 2). In adult females of different species of grasshopper, however, the average daily consumption depends on their weight. Individuals of two species differing greatly in size, e.g. *Mecostethus grossus* L. (body weight about 650 mg) and *Chorthippus dorsatus* Zett. (about 300 mg) were compared, while in the same physiological state (e.g. mature females). Daily consumption by smaller individuals proved to be greater by 0.2 mg of fresh grass mass per 1 mg of fresh mass of their body.

The amount of grass eaten by grasshoppers under the isolators was calculated on the basis of the above data.

2. Variations in number and biomass of grasshoppers under isolators

In order to intensify, and thus to make it easier to grasp, the influence of grasshoppers on the vegetation of the meadow, the initial densities of the insects introduced into the isolators were several times greater than the density of the insects in the meadow – 100, 300, 500 individuals per 0.64 m^2. These initial, artificially obtained, densities of the insects were not maintained for long. During the first 2–3 days a large number of insects died, the number vary with different initial densities.

Reduction of grasshoppers, i.e. the decrease in their number under the enclosed isolators, was caused solely by mortality. The course of such reduction with different initial densities is shown in Table I as the mean daily mortality in successive periods of the experiment.

Reduction of grasshoppers under isolators

Tab. I

Station	Initial density	Loss of individuals	Daily mortality	Loss of individuals	Daily mortality	Loss of individuals	Daily mortality	Loss of individuals	Daily mortality
Caricetum elatae (Mc)		period *I* (7–8 days)		period *II* (14 days)		period *III* (24 days)		period *IV* (11 days)	
	100	65	8.1	15	3.14	10	2.1	1	1.0
	300	202	8.4	53	3.9	30	2.8	11	7.3
	500	418	11.5	67	5.9	9	2.5	6	10.0
Stellario-Deschampsietum (D)		period *I* (1–2 days)		period *II* (14 days)		period *III* (22 days)			
	100	50	25.0	47	3.0	2	3.7		
	300	190	63.3	23	0.65	67	7.0		
	500	330	66.0	117	2.08	42	7.2		

During the first one- to several day period of the experiment mortality among grasshoppers under the isolators was greater, wherever the density of the insects was greater. On station *D* in the case of the two higher densities it was almost identical, and very high in comparison with the lowest density. On station *Mc*, with the two lowest densities it differed very slightly, and was only markedly greater at the highest density (Tab. I).

After this period of intensive reduction, mortality among grasshoppers in the isolators distinctly decreased in the case of all the densities and remained on a low level for a long time. It was not until the final phase of the experiment that the situation changed. In some isolators mortality dropped to zero, and density remained for a long time on a low level similar to the density found in the meadow. In others, mortality increased so greatly that all the grasshoppers died.

For about 6 weeks, however, despite the high and non-uniform mortality, the differences in density under the isolators, corresponding to the differences in initial density, remained, generally, unchanged (Tab. II).

Losses of grass under isolators with different densities of grasshoppers

Tab. II

Station	Initial density	Losses of grass under isolators (in g of dry mass)		Average density of grasshoppers	
		period *I*	period *II*	period *I*	period *II*
Mc	100	34.58	42.42	52.00	19.1
	300	63.70	4.55	151.7	34.1
	500	75.32	1.47	203.7	13.2
D	100	23.20	9.17	49.8	18.7
	300	45.76	8.27	123.0	71.0
	500	53.04	3.76	215.0	84.3

In order to calculate variations in the biomass of grasshoppers under the various isolators, we drew diagrams of variations in numbers of insects and of variations in weight of an average grasshopper during the experimental period (Fig. 3 *A* and *B*).

3. Amount of grass consumed by grasshoppers under isolators

These amounts were obtained by multiplying daily consumption per unit of weight of a grasshopper of a given size by the biomass of grasshoppers under the isolators on two stations (Fig. 3 *A* and *B*). In this way, the weight of grass eaten by grasshoppers during the experiment was obtained. The amounts of food consumed, calculated in this way, for the first and second period are given in Table III.

4. Effects of consumption by grasshoppers under isolators

Variations in the amount of primary production assessed in our experiment result from at least three factors: 1) consumption of plants by grasshoppers,

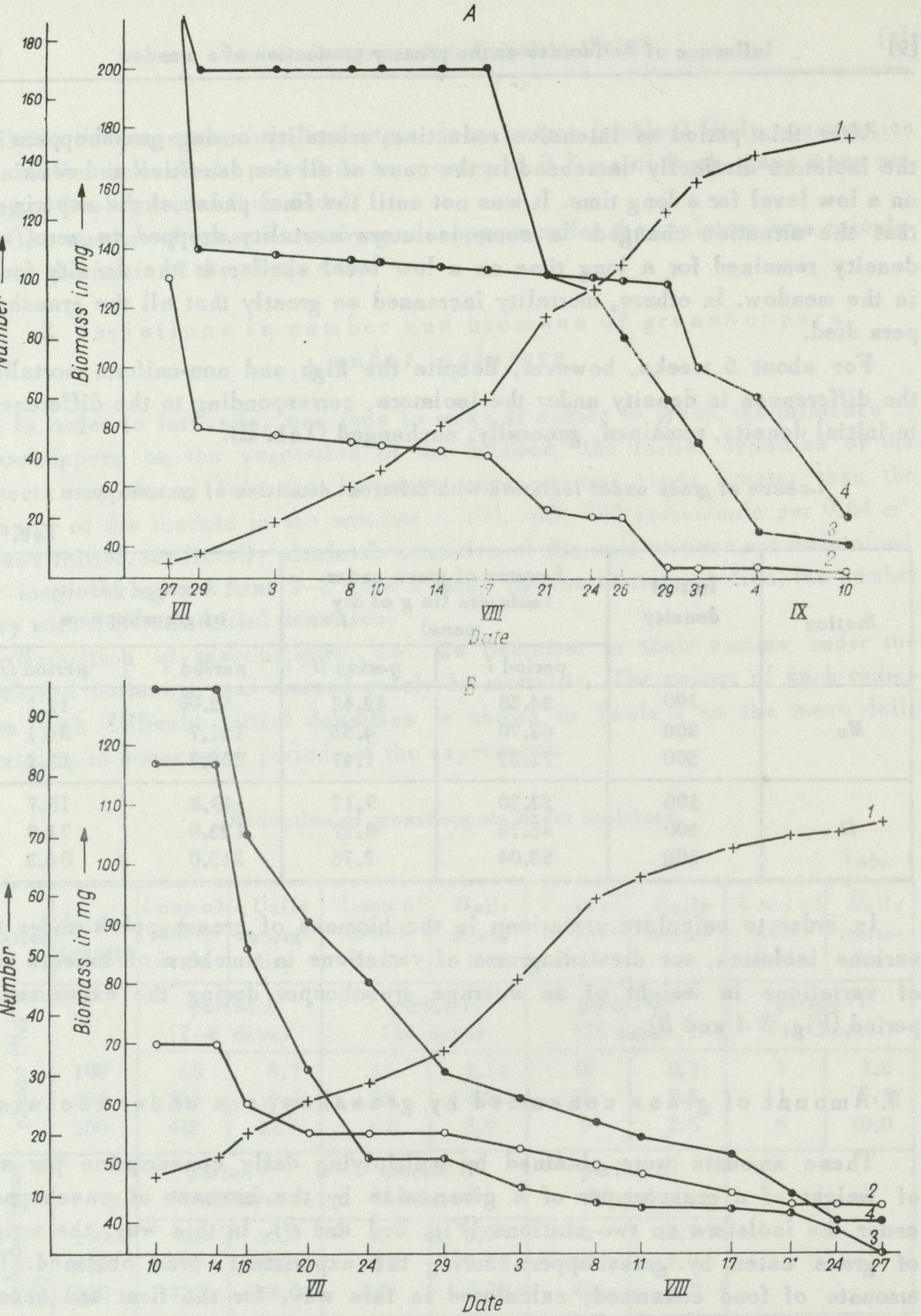

Fig. 3. Variations in number and biomass of grasshoppers during the experiment under isolators

A — on station *D*, *B* — on station *Mc*

1 — biomass of average grasshopper, *2* — number of grasshoppers under isolators with initial density of 100, *3* — number of grasshoppers under isolators with initial density of 300, *4* — number of grasshoppers under isolators with initial density of 500

Amount of grass consumed by grasshoppers under isolators calculated from food rations (g of fresh mass of grass)

Tab. III

Initial density	Amounts of grass consumed			
	station *D*		station *Mc*	
	period *I*	period *II*	period *I*	period *II*
100	7.17	5.16	6.14	2.75
300	17.17	33.33	17.14	2.55
500	27.46	29.56	20.12	3.01

2) destruction of uneaten parts of plants during feeding and 3) reaction of plants to the grasshoppers' activities. The amount of plant mass consumed by grasshoppers was assessed in the previous section (Tab. III).

Damage to plants

Let us consider now the losses due not to consumption but caused by portions of leaves breaking off or drying up as the result of being bitten. The longer the leaves on the plant on which they feed, the greater the losses due to drying up and falling of portions of leaves bitten by grasshoppers, even when the number of damaged parts is the same and their location on the leaves completely random. Plants used as a basis for assessing the losses in primary production caused by grasshoppers differ in length of leaf on the two working stations. The average length of the leaf blades of undamaged leaves on station *D* (*Stellario-Deschampsietum*) for the following three species examined (*Carex panicea, C. fusca, Deschampsia caespitosa*) was about 22 cm. On station *Mc* (*Caricetum elatae*) this was about 60 cm (average for *C. hudsoni* and *C. vesicaria*).

These differences affect the amounts of loss caused by grasshoppers feeding on the two stations. On station *D* during the first period of the experiment, of the total losses in primary production under isolators, only about 13% is due to consumption by grasshoppers. The remainder, i.e. about 87%, is formed by the unused remains of the plant. On station *Mc* the percentage of consumed food is on an average 8%, and of destroyed primary production – 92%.

The ratio of consumed to destroyed plant mass varies with different densities of grasshoppers and depends on the number of feeding insects and the time during which the habitat is used. With little destruction of the habitat, the percentage of biomass consumed in total plant mass losses is more or less stable. If we assume that daily consumption by grasshoppers is constant, regardless of the degree of destruction of grass under the isolators (Tab. IV), then during the second period of the experiment the percentage of consumption in total plant mass losses increases sharply with the density of insects and degree of destruction of the habitat.

Losses in primary production due to consumption (calculated) by grasshoppers (in %)

Tab. IV

Initial density	Station *D*		Station *Mc*	
	period *I*	period *II*	period *I*	period *II*
100	10	18	6	2
300	13	134	9	41
500	17	262	9	68

On station *D*, in the isolators with two high densities of insects, where plants forming the grasshoppers' food has been destroyed, losses in plant production are lower than the food requirements of the grasshoppers living under these isolators. When calculated for one individual, the amount of plant losses on station *D* during the first feeding period (3 weeks) was similar, with initial densities of 100 and 300 individuals per isolator, and was 26 and 21 mg of dry mass of grass per individual per day (Tab. V). With continued feeding by the grasshoppers on grass already intensively bitten, however, daily losses in gras per individual remained on more or less the same level (20 mg of dry mass of grass per individual per day) only with the smallest density (on an average about 19 individuals per isolator). Under this isolator there was relatively little destruction of grass. In isolators with higher densities, where after the insects had fed on grasses and sedge only "stubble" was left, and at the end only the dicotyledonous plants which grasshoppers do not eat grew above the moss, losses could not be great (Tab. V). With longlasting high density of grasshoppers (71 from the initial number of 300) the amount is 4.5 mg of dry mass of grass per individual per day. With even higher density (84 individuals from an initial number of 500) the amount is 1.7 mg of dry mass per individual per day. In comparison with the daily food requirements of the average individual under the isolator, which was 5–6 mg of dry mass of grass, this is a starvation ration.

Losses in plants, defined from samples taken under the isolator after the insects had been feeding for about 3 weeks, are compared with the numbers of the grasshoppers feeding during these periods (Fig. 4 *A* and *B*). With lesser densities losses in grass are in proportion to the density of the grasshoppers. With greater densities, when considerable destruction of the habitat takes place, losses in plant mass per individual are increasingly smaller and the grasshoppers finally starve (Fig. 5).

Destruction of grass under isolators with different densities of grasshoppers (per 1 individual)

Tab. V

Station	Initial density	Destruction of grass			
		per individual per day (in g of dry mass of grass)		in relation to control samples (in per cent)	
		period *I*	period *II*	period *I*	period *II*
Mc	100	0.036	0.126	35	58
	300	0.023	0.008	65	50
	500	0.021	0.007	77	59
D	100	0.026	0.020	39	55
	300	0.021	0.005	77	91
	500	0.14	0.002	89	95

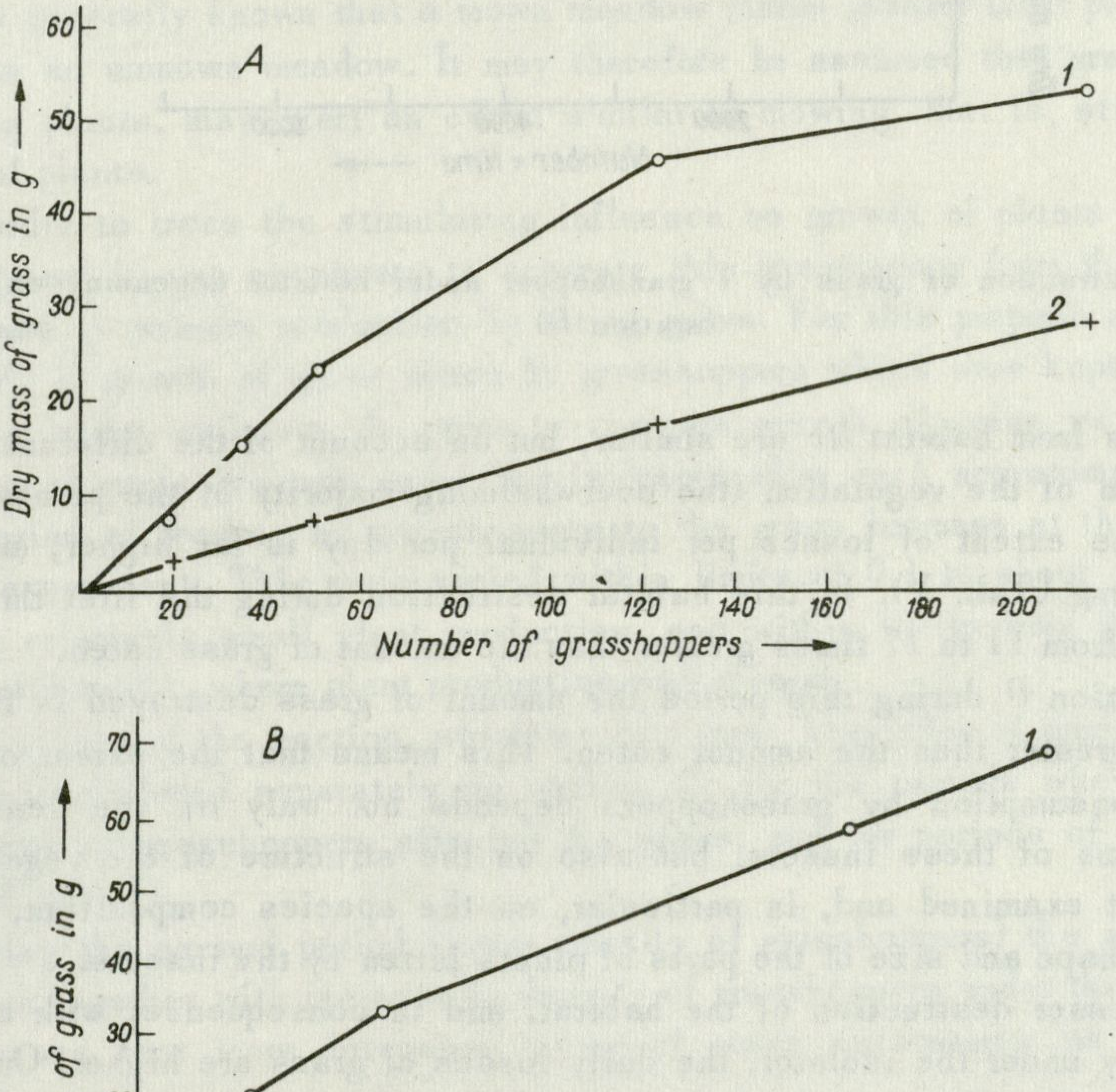

Fig. 4. Relation between mass of grass consumed and destroyed and density of grasshoppers under isolators over 3 weeks
A – on station *D*, *B* – on station *Mc*
1 – grass eaten and destroyed, *2* – grass eaten

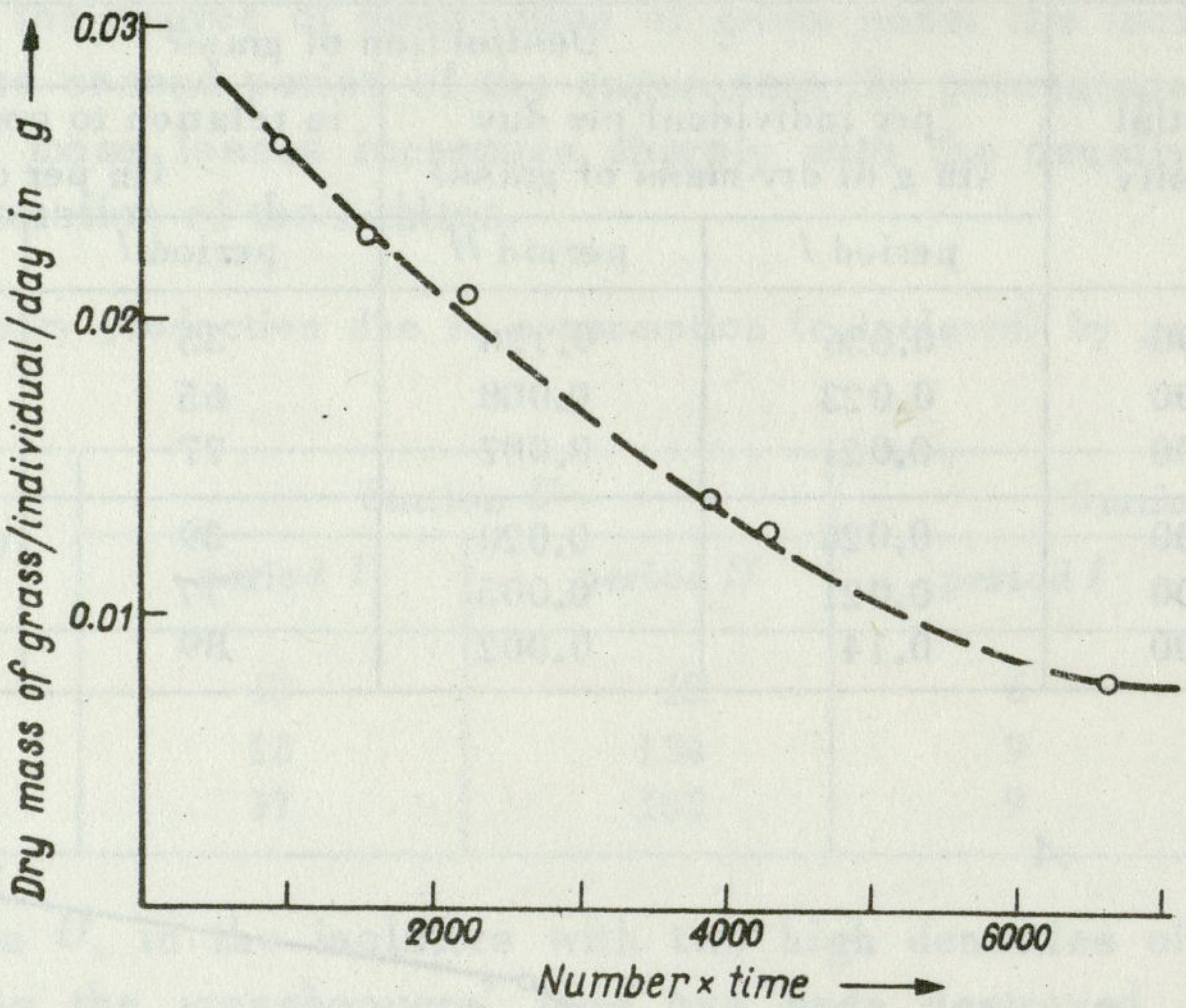

Fig. 5. Destruction of grass by 1 grasshopper under isolator depending on numbers (station *D*)

Results from habitat *Mc* are similar, but on account of the different species composition of the vegetation (the overwhelming majority of the plants are tall sedges) the extent of losses per individual per day is far higher, amounting to 7–126 mg (Tab. V). In this habitat destruction during the first three-week periods is from 11 to 17 times greater than the amount of grass eaten.

On station *D* during this period the amount of grass destroyed is from 6 to 10 times greater than the amount eaten. This means that the extent of losses due to consumption by grasshoppers depends not only on the density and feeding time of these insects, but also on the structure of the vegetation in the habitat examined and, in particular, on the species composition, and the resulting shape and size of the parts of plants bitten by the insects.

With lesser destruction of the habitat, and in consequence, with a greater food supply under the isolator, the daily losses of grass are higher. On station *D* with considerable excess of food, or with the least density (initial density 100), losses of grass per one grasshopper are high and independent of the amount of food available. With higher densities the ratio of biomass of grasshoppers to fresh mass of grass under the isolators is less favourable (and deteriorates further with their continued feeding during the second period of the experiment).

The extent of grass losses due to feeding by grasshoppers is determined by the ratio of biomass of phytophages to potential food supplies under the isolators, which differs on the different working stations we examined. With excessive densities, with which the ratio of number and biomass of phytophages to the potential food biomass is unfavourable to the insects, the grasshoppers reduce their daily food rations, and even starve, long before all the food supplies are exhausted.

The amount of food consumed by grasshoppers (and therefore reduction in the food resources which are limited in the isolator) is to a certain extent dependent on the amount of these resources, increasing (within certain limits) with increase in food supply.

Activities of phytophages stimulating the growth of plants

It is generally known that a mown meadow yields greater total plant production than an unmown meadow. It may therefore be assumed that grasshoppers, by biting plants, may exert an effect similar to mowing, that is, stimulate the growth of plants.

In order to trace the stimulating influence on growth of plants exerted by grasshoppers it was necessary to separate this phenomenon from the reduction they cause in primary production by biting grass. For this purpose an analysis was made of growth of grass bitten by grasshoppers which were kept in varying densities under isolators. In order to compare growth of grass we calculated the ratio of grass biomass under the isolators after each approximately three-week period of feeding by grasshoppers to the grass biomass at the beginning of the experiment. This ratio varied within limits of 0.1 to about 1 on station *D*, with relatively small plant production, and within limits from 0.2 to about 2.5 on station *Mc*, where plant production was greater.

The values of the fraction, which we may term "the index of grass growth", must be considered separately on station *Mc* for the periods when high concentrations of grasshoppers affected the grass, and for periods of lesser densities (Fig. 6 *A*).

During the second period (lower density of grasshoppers) the growth index increases together with increase in density of grasshoppers under the isolators. This means that more intensive biting of grass encourages its more rapid regrowth.

With high densities of grasshoppers, however, (first period) there is a decrease in the index corresponding to increase in the density of the insects. In this case the more the grass is bitten, the weaker the regrowth. Probably very badly damaged plants (with the greater part of the leaf blades bitten off), are thus deprived of their assimilation surface, and incapable of regrowth. In such case the grasshoppers exert a one-sided effect on plants, that is, they only lower production of green mass and destroy the reaction of the plant expressed in acceleration of growth.

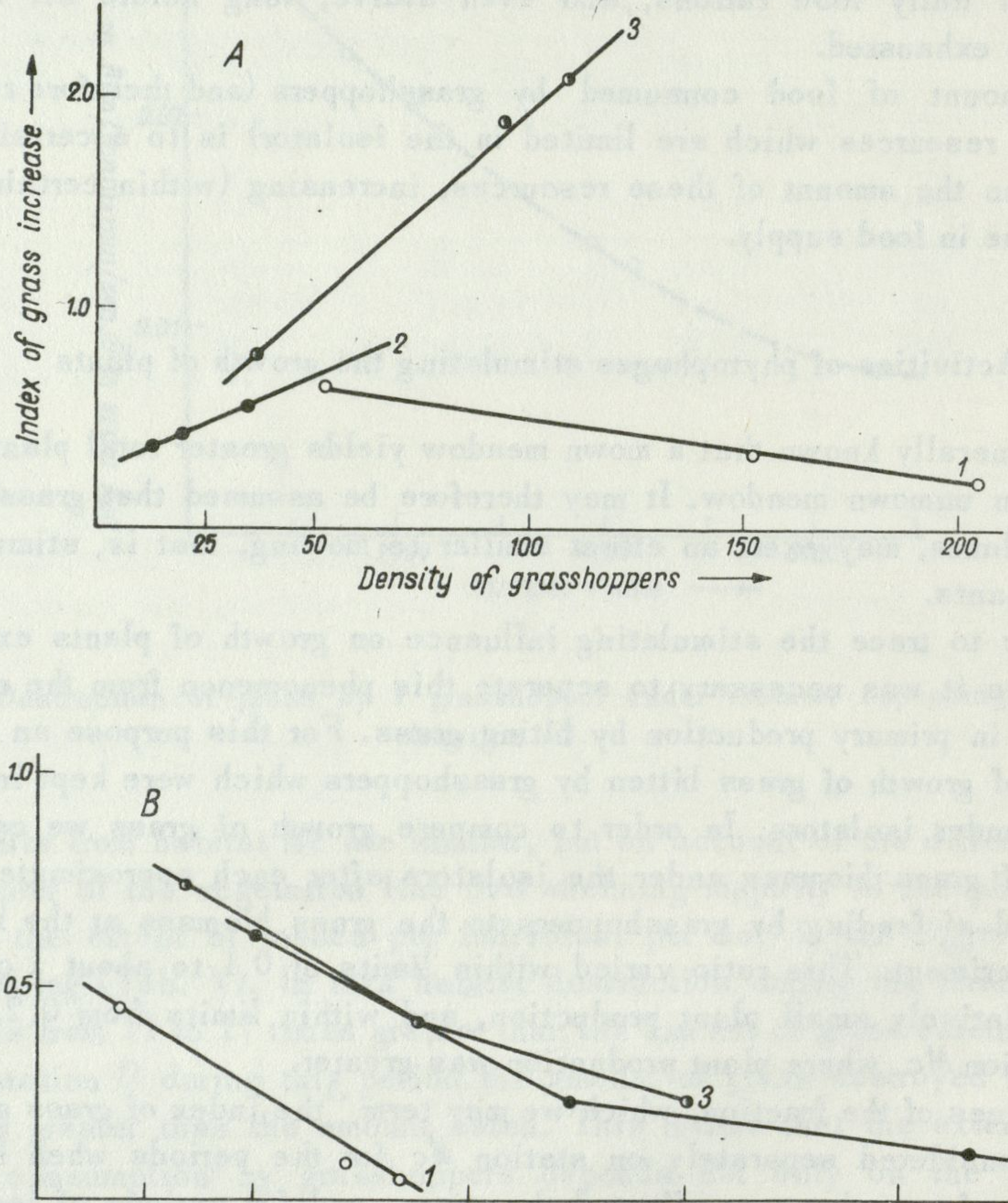

Fig. 6. Index of grass increase depending on density of grasshoppers

A – on station *Mc*, *B* – on station *D*

1 – for first 3-week period of feeding, *2* – for second 3-week period of feeding, *3* – after six weeks of feeding

Regrowth of plants depends not only on the intensivity with which they are bitten by grasshoppers, but also on the time of the year, and thus on whether regrowth of grass is possible at the given time. The analysis of primary production made in the Strzeleckie Meadows by Traczyk (1968) shows that maximum growth of green mass occurs in June and July. In August and September the amount of plant mass produced begins to decrease. On station *Mc* isolators were set up early and the experiment coincided with the period of intensive growth of plants. Even with high densities of grasshoppers complete destruction of vegetation never took place.

On station *D* plant production, in particular production of plants used by grasshoppers, is far lower, and thus the relative densities of the insects were higher than on station *Mc*. What is more, the isolators were set up later, during the period of minimum growth of the plants. Under these conditions the index of growth of grass throughout the whole duration of the experiment decreased together with increase in density of grasshoppers (Fig. 6 *B*). The plants were unable to replace the losses sustained. The effect of the grasshoppers on the habitat was one-sided, that is, destructive.

V. ROLE OF GRASSHOPPERS IN REDUCING PLANT PRODUCTION OF THE MEADOW

The density of grasshoppers feeding on the study areas of the meadow was assessed from quantitative samples taken once a week from spring to late autumn. Mean density of grasshoppers and their average biomass for each month was computed. Also the amount of grass the insects consumed in successive months was calculated from their daily food rations (Tab. VI).

On station *D* grasshoppers which had fed there for 4 months had eaten about 5 g of dry mass of grass per m^2 of meadow. On station *Mc* the grashoppers living there had eaten about 4.6 g of dry mass of grass per m^2. The weight of the grass destroyed by the grasshoppers must be added to the weight of grass which they consumed.

Experiments to assess the ratio of biomass of grass consumed by grasshoppers to that destroyed by them were made only for insects weighing more than 60 mg. For such insects the amount of grass consumed on station *D* was on an average 13% of the total losses of grass (sum totals of weight of consumed and destroyed grass); on station *Mc* the average was 8%. The weight of plants destroyed by individuals more than 60 mg in weight, mainly mature individuals, was added to the sum total of losses in plant mass caused by the insects' feeding.

On station *D* losses of grass (eaten and destroyed) caused by the grasshoppers living there were assessed as about 24 g of dry mass of grass per m^2, which forms 14% of total primary production of vascular plants of the *Stellario-Deschampsietum* association. On station *Mc* losses in vegetation were assessed as 45 g of dry mass of grass, i.e. about 8% of the total primary production of the *Caricetum elatae* association.

VI. CONCLUSIONS

The following results were obtained from experimental observations made in a meadow habitat of the "phytophage – plant" relation:

The extent of damage caused by the grasshoppers' biting plants depends on the density of the insects, their feeding time and the properties of the vegetation cover and of plants on which these insects feed.

Plant losses are, generally, in proportion to the density of the grasshoppers. When, however, the density of these insects is so great that destruction of

Amount of grass consumed by grasshoppers per 1 m² under natural conditions in the meadows examined (calculated from values obtained in the meadow and in the laboratory)

Tab. VI

Month	$\bar{x}$ density	$\bar{x}$ biomass of 1 individual in mg	$\bar{x}$ biomass of grasshoppers in mg	Food ration in mg of dry mass	Grass consumed over whole month in g
Caricetum elatae					
VI	10.0	29.0	290.0	0.126	1.090
VII	8.4	66.5	558.6	0.075	1.299
VIII	10.0	87.5	875.0	0.061	1.649
IX	3.2	122.5	392.0	0.050	0.588
Jointly during period of experiment					4.626
Stellario-Deschampsietum					
VI	18.0	15.0	270.0	0.163	1.318
VII	8.4	33.5	281.4	0.105	0.915
VIII	9.7	101.5	984.5	0.052	1.526
IX	8.6	172.0	1479.2	0.030	1.331
Jointly during period of experiment					5.090

the habitat reaches 80 or more per cent, losses of plants per grasshopper may be smaller than the insect's daily food requirements. Under conditions of overcrowding the grasshoppers starve, despite that fact that there is a certain small amount of food still left in the habitat. With limited and small food supply in the habitat the amount consumed by grasshoppers depends on the amount of the supply.

Extent of destruction due to grasshoppers is also affected by the type of vegetation, and above all by the shape and length of the leaves bitten. Serious damages to the leaves made when feeding along the whole length of the leaf cause the leaves either to fall or at least the greater parts of them to dry up. Comparison of the extents of losses in green mass of plants with the amount of mass of grass eaten by grasshopper shows that in a habitat in which the plants have shorter leaves (*Stellario-Deschampsietum*) destruction, depending on the insects' density, is on an average 6 times greater than the amount of grass eaten, and may be as much as ten times greater. In a habitat in which mainly tall plants occur (*Caricetum elatae*) destruction is on an average 15 times greater than the amount of mass consumed, and this ratio may be as much as 25. The longer the bitten leaves, the larger the area of these leaves which is destroyed.

Experimental data made it possible to calculate the losses incurred in primary production as the result of consumption by grasshoppers under natural conditions. In the wet meadow plant association, *Stellario-Deschampsietum*, with average density of 10 feeding insects per m^2 for 4 months, losses in primary production are about 24 g of dry mass of grass, which reduces the primary production of the meadow by 14%.

In the association of tall sedges (*Caricetum elatae*) an average of 7 individuals per 1 m^2 feed for 3 months. They eat and destroy 44.1g of the dry mass of grass and in consequence reduce the primary production of the meadow by 8%.

Biting of grass by grasshoppers not only causes losses in green mass of plants but may also increase grass production by stimulating more intensive growth. The stimulating effect of grasshoppers on plants is strongest in early summer, during the period of maximum growth of grasses. The extent of grass growth also depends on the amount of green mass of plants removed by the insects. Plants react to more intensive biting of the leaves by more intensive growth, if of course the plants have not been completely destroyed.

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WPŁYW *ACRIDOIDEA* NA PRODUKCJĘ PIERWOTNĄ ŁĄKI (EKSPERYMENT TERENOWY)

Streszczenie

Zestawiono wyniki eksperymentalnej oceny wpływu owadów roślinożernych na roślinność łąki. Zależność „roślinożerca – roślina" badano na przykładzie szarańczaków, owadów zgryzających rośliny. Jest to jedna z dominujących grup owadów roślinożernych w tym środowisku.

Badania prowadzono w dwu zespołach roślinnych: *Stellario-Deschampsietum* Freitag 1959 i *Caricetum elatae* W. Koch 1926, na śródleśnej łące w Puszczy Kampinoskiej.

Reakcję roślinności łąkowej na działanie owadów roślinożernych badano w izolatorach z gazy rozpiętej na szkielecie z drutu, ustawionych na łące, na której równolegle badano dynamikę liczebności i biomasy tych owadów. Dzienne spożycie owadów o różnej biomasie znane było z hodowli laboratoryjnych.

Jak wynika z przeprowadzonych badań, wielkość uszkodzeń powodowanych zgryzaniem przez szarańczaki zależy od zagęszczenia owadów, czasu żerowania oraz właściwości szaty roślinnej i roślin, którymi te owady się żywią.

Ubytki roślin są na ogół proporcjonalne do zagęszczenia szarańczaków. Kiedy jednak zagęszczenie szarańczaków jest tak duże, że zniszczenie środowiska sięga 80% i więcej, ubytki roślinności przeliczone na jednego szarańczaka mogą być mniejsze

od jego dziennego zapotrzebowania pokarmowego. W warunkach przegęszczenia szarańczaki głodują, mimo że w środowisku znajdują się jeszcze pewne niewielkie ilości pożywienia. Przy ograniczonych i małych zapasach pokarmu w środowisku wielkość konsumpcji szarańczaków jest zależna od wielkości tych zapasów.

Na wielkość zniszczeń powodowanych przez szarańczaki wpływa również typ roślinności, a przede wszystkim kształt i długość zgryzanych liści. Głębokie wyżerki pozostawione przez szarańczaki na całej długości liścia powodują odpadanie lub co najmniej obsychanie jego dużych części. Porównanie wielkości strat w zielonej masie roślin z ilością masy trawy zjedzonej przez szarańczaki wskazuje na to, że w środowisku, w którym rośliny mają liście krótsze (*Stellario-Deschampsietum*), zniszczenie, w zależności od zagęszczenia, jest średnio 6 razy większe od ilości zjedzonej trawy i może dochodzić do dziesięciokrotnie większego. W środowisku, w którym występują głównie rośliny wysokie (*Caricetum elatae*) zniszczenie jest średnio 15 razy większe od ilości zjedzonej masy, a stosunek ten może dochodzić do 25 Im wygryzane liście są dłuższe, tym większa ich część ulega zniszczeniu.

Dane eksperymentalne pozwoliły na obliczenie strat w produkcji pierwotnej na skutek żerowania szarańczaków w warunkach naturalnych. W zespole roślinnym łąki wilgotnej (*Stellario-Deschampsietum*), przy średnim zagęszczeniu 10 owadów żerujących na 1 m^2 przez 4 miesiące, straty produkcji pierwotnej wynoszą około 24 g suchej masy trawy, co zmniejsza produkcję pierwotną łąki o 14%.

W zespole wielkich turzyc (*Caricetum elatae*) na 1 m^2 żeruje przeciętnie 7 osobników w ciągu 3 miesięcy. Zjadają one i niszczą 44 g suchej trawy i tym samym obniżają produkcję pierwotną łąki o 8%.

Zgryzanie trawy przez szarańczaki nie tylko powoduje ubywanie zielonej masy roślin, ale może również zwiększać ich produkcję prowokując intensywniejszy ich wzrost. Stymulujący wpływ szarańczaków na rośliny najsilniejszy jest wczesnym latem w okresie maksymalnego wzrostu trawy. Wielkość przyrostów trawy zależy wtedy również od ilości usuniętej przez szarańczaki zielonej masy roślin. Na silniejsze zgryzanie liści rośliny reagują silniejszym wzrostem, o ile oczywiście nie doszło do zniszczenia samych roślin.

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