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EGG REDUCTION OF THE COLORADO BEETLE
(*LEPTINOTARSA DECEMLINEATA* SAY)
AS A HUNGER-DEPENDENT REACTION

The egg reduction of the Colorado beetle is not dependent on density. The number of eggs destroyed by predators in the period of the maximal egg density is lower than for minimal densities. There is no correlation between the number of aphidophages and the egg reduction. The destruction of the Colorado beetle eggs is a hunger-dependent reaction, aphidophages devour eggs of the Colorado beetle because of the deterioration of their alimentary conditions, i.e. when the density of aphids is low.

The aim of the present paper is to clarify by way of quantitative investigations the connection between the egg reduction of the Colorado beetle (*Leptinotarsa decemlineata* Say) and the functioning of the relationship aphids - aphidophages in the potato field.

Among numerous publications on the subject of the Colorado beetle a singularly small number of analyses concerning the problem of the biocenotic reduction in local populations is striking. A list of the Colorado beetle enemies set up for the whole area of this species (Węgorzek 1959) is quite sizable, however the number of reliable pieces of information on the effect of any of them on the reduction of specific populations of the Colorado beetle is relative-

ly small. Elaborations concerning parasites *Phorocera doryphorae* Riley (Bogdanov-Katkov 1947) and worms from the genus *Mermis* (Lisner and Beck 1955) may be treated as exceptions. Failures in the organization of the biological control of the Colorado beetle led to the formation of doubts in the existence of any environment resistance against this species and gave rise to the conception of helplessness of the biocenose as far as the Colorado beetle is concerned. In Europe this conviction was consolidated after abortive attempts to check the invasion of the Colorado beetle in France (Trouvelot 1931 and Feytaud 1939) with the help of introduced and local species of potential enemies of the Colorado beetle. Together with the Colorado beetle the idea of helplessness of the biocenose passed to Germany where abortive attempts in the acclimatization of American enemies (Sellke and Winnig 1939) and the lack of belief in the effectiveness of birds as the Colorado beetle enemies (Boback 1950) caused the acceptance of this idea as proved.

In Poland similar views were put forward by Węgorzek (1957, 1959) who argued that the specific characteristic of the Colorado beetle reveals itself in the fact that there has not been found any concrete biocenetic elements which could be used in the control of this pest. But arguments associated with this concept suffer two disadvantages: the lack of any data on the course of reduction of the Colorado beetle in nature and the lack of information on actual biocenotic connections of this species.

Not very numerous quantitative investigations concerning the reduction of the Colorado beetle (Kaczmarek 1955, van den Bruel and Moens 1959, Karg and Trojan 1968) enabled to state that the natural reduction of the Colorado beetle excluding the chemical control has a permanent, characteristic course and includes as a rule a few scores of percent of individuals. The observed regularities indicate the necessity of further investigations explaining in a quantitative way the biocenotic conditioning of the Colorado beetle. In spite of the statements put forward so far (Węgorzek 1957) potato fields on which the Colorado beetle appeared absorbed the pest from behind the ocean disregarding the fact whether they were prepared or not. In recent years the intensity of appearances of this species in Poland (Węgorzek and Piekarczyk 1965) becomes less and less dangerous to agriculture. It seems quite possible that several years of contacts of this species with the biocenose of the potato field was enough to give rise to adaptation inside the biocenose enabling an inclusion of the Colorado beetle population in the energy flow in agrocenose. However these problems require further investigations.

AREA AND METHODS

Our investigations were carried out in 1965 on two potato fields situated at the State Farm Rogaczewo in Wielkopolska. In both the fields the same crop rotation had been applied for a number of years and no chemical control had been carried out in this area. The soil of the two fields consisted of average sand on clay and about 40,000 potatoes of the „Lenino” variety were planted per one hectare. The potatoes shot up at the end of May and were dug up at the end of September.

In the course of the whole vegetative season the following pieces of information were collected from the two fields:

1. Estimate of the number of laid and destroyed eggs. It was carried out every three days, each time on 120 potato plants chosen at random on the field according to a previously elaborated system (Karg and Trojan 1968). All the egg layers found during the review of plants were taken to the laboratory and there the number of laid and destroyed eggs was determined with the help of a microscope. The observed number of destroyed eggs (r) in view of the nine-days period of the egg development in 1965 did not correspond with the egg reduction in the course of the whole of their development. Separate egg layers were exposed to predators on the average for four or five days. In order to obtain a more complete picture of the egg reduction in the course of the whole period of their development the observed number of destroyed eggs was doubled ($2r$).

2. Estimate of the number of aphids. Data were collected with the method of fifty leaves and the average number of aphids per one potato sprout was estimated. A series of samples consisted of fifty sprouts and was collected once a week. The density of aphids per 1 m^2 was calculated by multiplying the number of aphids on the sprout by the number of sprouts recorded in the given period on 1 m^2 .

3. Estimate of the number and density of aphidophages. Data concerning specific composition and partly the number of lady-birds were based on the materials collected from specially chosen plants and similarly as with aphidophage bugs on the materials obtained from the quantitative scoop. Density was determined by the use of a special biocenometer applied in our entomologic investigations (Gromadzka and Trojan 1967). A series of captures consisting of ten samples was collected every ten days from the two fields.

REGULARITIES IN THE EGG REDUCTION OF THE COLORADO BEETLE

In field experiments concerned with the egg reduction of the Colorado beetle at densities selected in an experimental way Kaczmárek (1955)

proved some connection between the egg reduction of the Colorado beetle and their density. In our investigations we found out that there occurred a connection of a similar character (Fig. 1). And so in completely natural conditions dependence $y = a : x$ (Kaczmarek 1955) was supported by evidence. However this dependence has a somewhat disquieting character from the biological point of view. The number of reduced eggs (a) did not show any dependence on their density ($a = \text{const.}$). In such a situation the observed dependence would have an apparent character and would follow only the way in which the obtained information had been set up.

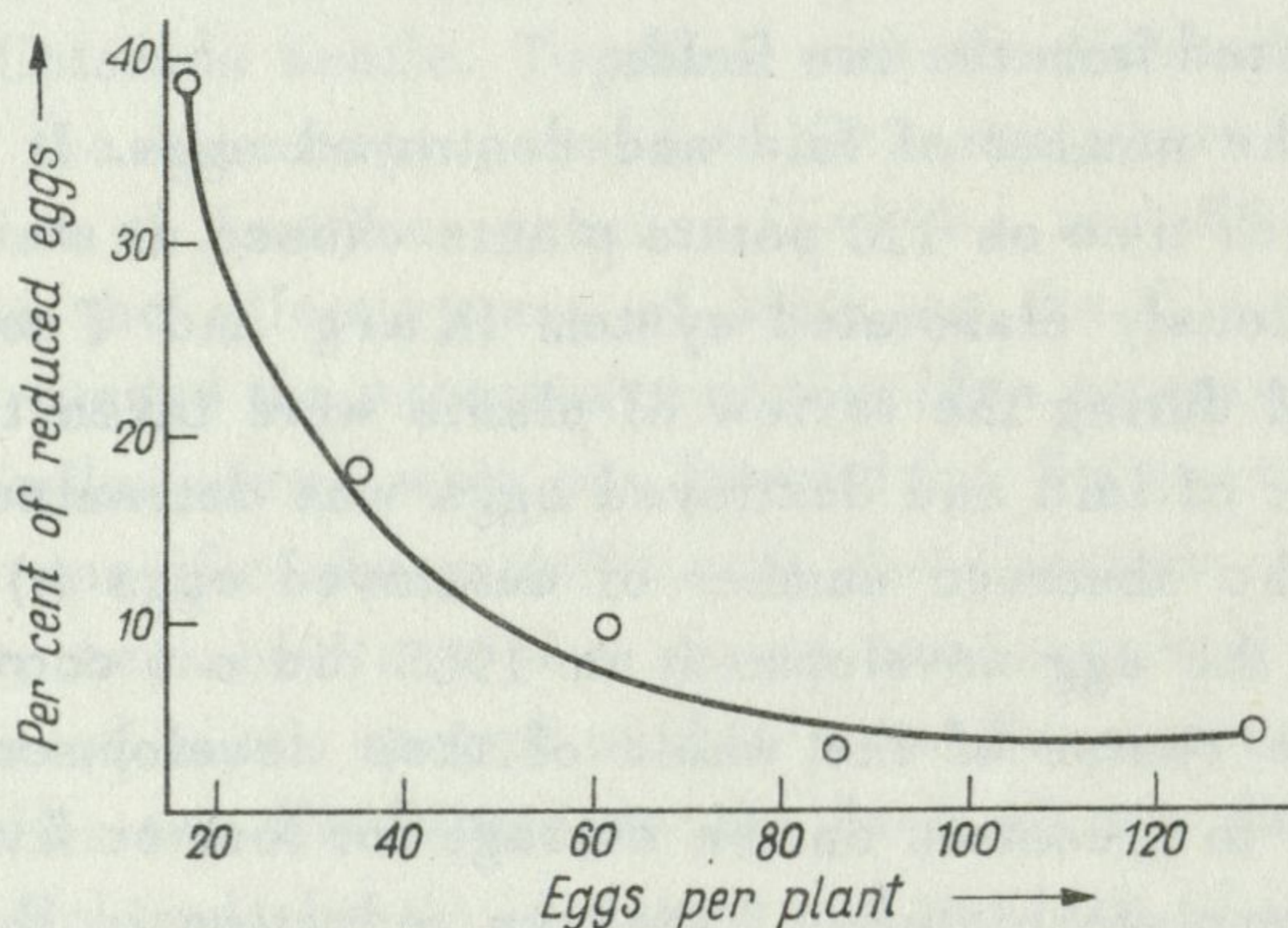


Fig. 1. Interrelation between density and reduction of eggs of the Colorado beetle

Our further considerations were based not only on the per cent but also on the number of reduced eggs. This figure showed in July experiments carried out by Kaczmarek (1955) a simple dependence which may be presented in the form of a formula:

$$r_n = a + 0.1n \quad (1)$$

where: r_n – number of reduced eggs at their given density, a – egg reduction in the experiment with the lowest density ($a = 10$), n – number of eggs used in successive experiments.

The application of this function to the calculation of the number of reduced individuals (Tab. I) showed a far reaching conformity of the real reduction with the estimates obtained by the application of mathematical methods. The observed regularity was not of universal character and already in the next experiment (Karg and Trojan 1968) the number of reduced eggs may be roughly estimated with the help of the formula:

$$r_n = r_{n-1} - 0.02n \quad (2)$$

where r_{n-1} – number of eggs destroyed at a lower density (the remaining explanations see above).

An estimate of the real and calculated with the help of formula (2) number of eggs, destroyed at separate densities, (Tab. II) demonstrated a considerable similarity in the sphere of lower densities and an insignificant overestimate of the existing reduction at higher densities. After accepting the above mentioned reservations we may pass on to consider the ecologic significance of the above analysed function.

Interrelation between the reduction of the Colorado beetle and initial number of eggs on experimentally infested potato plants

Tab. I

	Number of eggs per potato plant				
Reduction	10	15	25	35	45
$r_n = 10 + 0.1n$	11	11.5	12.5	13.5	14.5
Real values	10.0	11.4	12.7	13.6	14.8

Interrelation between the reduction of the Colorado beetle eggs and initial number of eggs on naturally infested potato plants

Tab. II

	Number of eggs per potato plant					
Reduction	20	40	60	80	100	120
$r_n = r_{n-1} - 0.02n$	14.0	13.2	12.0	10.4	8.4	6.0
Real values	14.0	13.2	12.0	7.2	7.0	8.4

The value of the final member of the function ($+0.1n$ and $-0.02n$) is the factor indicating the ecologic situation of the investigated phenomenon of the egg reduction of the Colorado beetle. In the case of experimental densities (Kaczmarek 1955) a positive effect of density on the egg reduction was observed – about 10% of the increase in the number of eggs in these experiments was reduced. The egg reduction showed in these experiments a weakly positive character depending on density. An increase in the alimentary base boosted interest in this form of food which eggs of the Colorado beetle are for predators occurring on potato fields. However a different situation was recorded in the case of the course of natural reduction observed in 1965. Value ($-0.02n$) indicates that together with an increase in the density of eggs of about 2% there was a drop in the number of reduced eggs. And so we found out

in nature the situation in which an increase in the alimentary base was accompanied by a decrease in the attractiveness of food and as a result a less intensive destruction of eggs of the Colorado beetle.

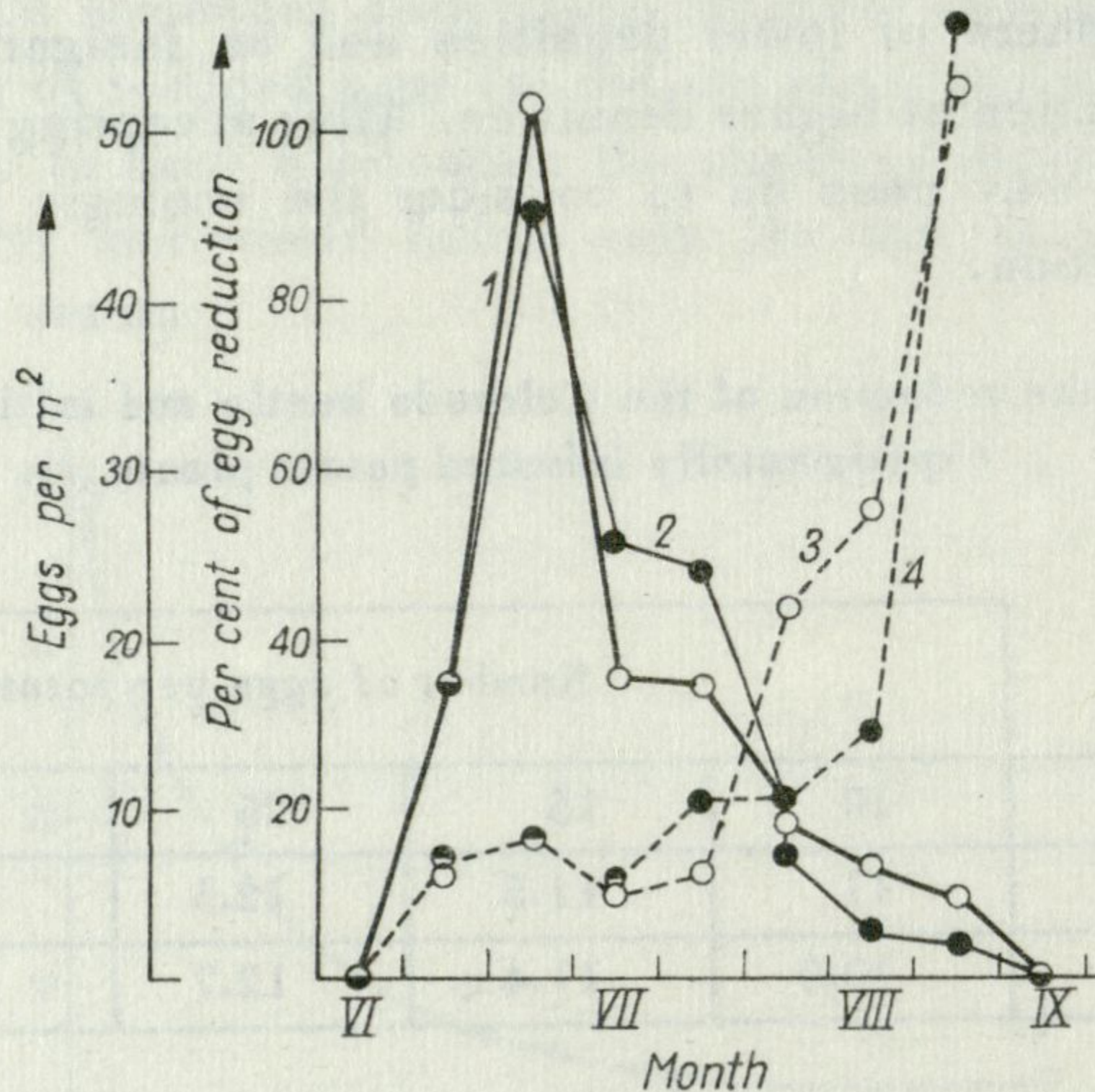


Fig. 2. Density and reduction of eggs of the Colorado beetle in two potato fields. Density: 1 — eastern field, 2 — western field; reduction: 3 — eastern field, 4 — western field

The course of the egg reduction of the Colorado beetle presents quite a different picture when time aspect is taken into consideration (Fig. 2). In 1965 on the two investigated fields the beginning of egg laying fell on the last ten days of June and the highest number of eggs was recorded at the beginning of July. In this period there occurred about fifty eggs per 1 m^2 . During the whole of July and August the number of laid eggs was getting smaller. The egg reduction against the background of their appearance looked as follows. The period when the highest number of eggs was recorded — July — was characterized by a low egg reduction, and only in August when the number of the Colorado beetle eggs was small the per cent of the reduced eggs went clearly up. A considerable increase in the number of destroyed eggs was not here of an apparent character because on one of the investigated fields the number of destroyed eggs was twice as high as the corresponding number in the previous period.

The above quoted data form a sort of paradox from the ecological point of view. For it has been observed that an increase in the attractiveness of the Colorado beetle as an alimentary basis occurred at the moment when the density of eggs was at the lowest point during the whole productive season and decreased as the time went by. Such an ecologic situation may be explained only if it is referred to biocenotic principles.

A hypothesis has been put forward according to which the Colorado beetle eggs on potato fields form a functional part of the biocenotic complex of aphids and aphidophages. Actual quantitative relations between the two components decided the intensity of the Colorado beetle eggs. Such opinion has been supported by both former (Bogdanov-Katkov 1947) and more recent (Kaczmarek 1955) observations on the devouring of the Colorado beetle eggs by aphidophages, however in the literature on the subject, so far as it is known to me, investigations on the reduction of the Colorado beetle eggs were not connected in any way with the information concerning the abundance of aphids and aphidophages.

CHANGES IN NUMBERS OF APHIDS AND APHIDOPHAGES

Aphids from the investigated fields were represented by four species: *Aphis nasturtii* Kalt., *A. frangulae* Kalt., *A. fabae* Scop. and *Myzus persicae* Sulz., but the two first were dominant and the two remaining formed the minority which did not exceed 2% of the total number of aphids and occurred at the beginning of the potato vegetative period more or less till the middle of July.

The appearance of aphids on the two fields had a slightly different character. On the eastern field in July a rapid increase in the number of potato aphids was observed and at the end of that month their density exceeded a thousand individuals per 1 m². Since the beginning of August there had occurred a sudden drop in the number of aphids (Fig. 3) and in the course of ten days their density came down to be less than a hundred individuals per 1 m². About 20th August the appearance of aphids on this field was eliminated.

On the western field (Fig. 3) the appearance of potato aphids lasted considerably longer and was characterized by two peaks, at the beginning and at the end of July. The density of aphids during these two peaks was twice as low as the one on the eastern field.

Aphidophages were represented by nine species of lady-birds: *Coccinella septempunctata* L., *C. quinquepunctata* L., *Adonia variegata* Goeze, *Propylaea*

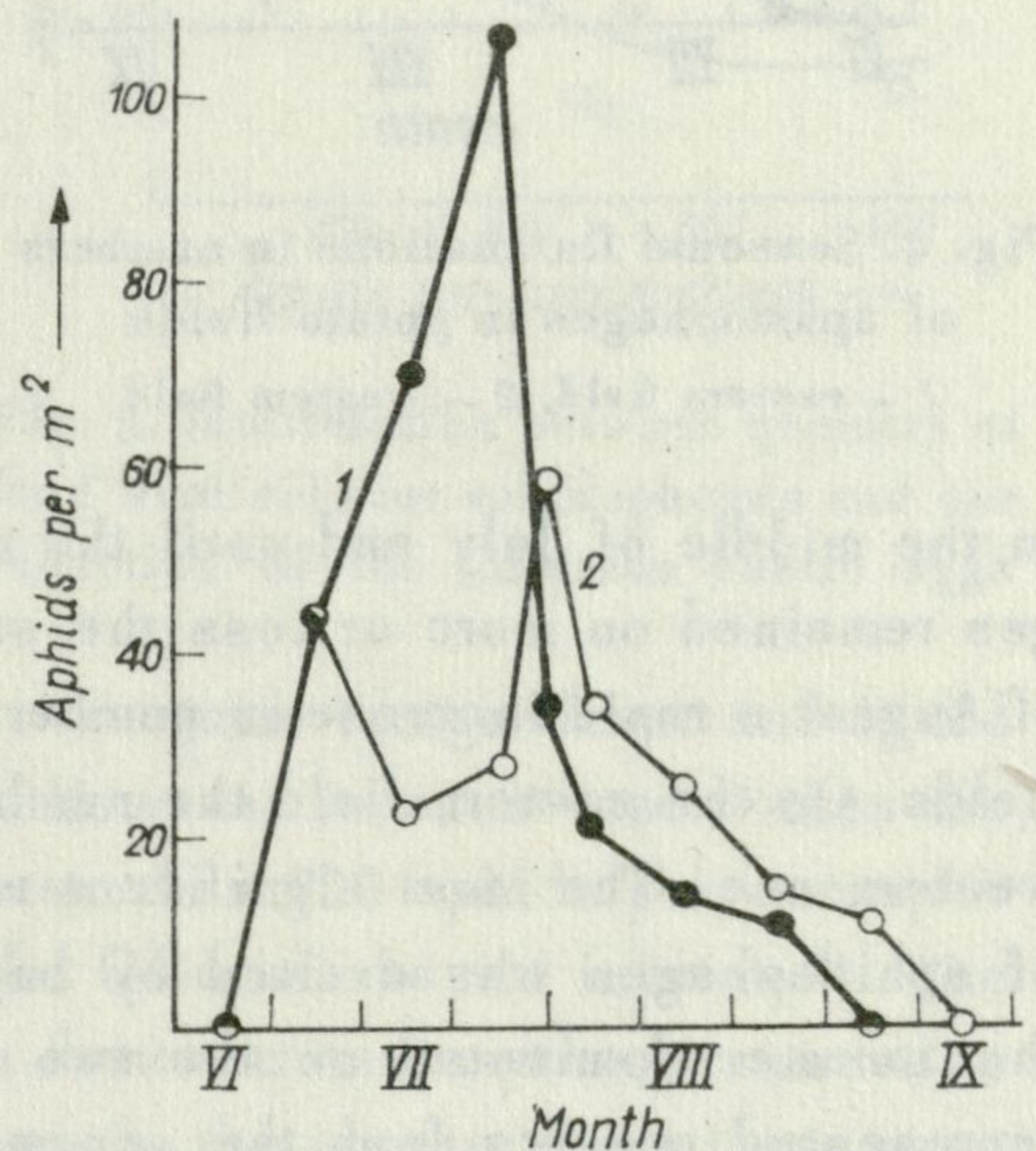


Fig. 3. Seasonal fluctuations in numbers of aphids in the potato field

1 — eastern field, 2 — western field

quatuordecimpunctata L., *Thea vigintiduopunctata* L., *Thytaspis sedecimpunctata* L., *Coccinulla quatuordecimpustulata* L., *Adalia bipunctata* L., and *Hippodamia tredecimpunctata* L. All these species occurred both as adult individuals and as larvae. Beside lady-birds also a number of species of bugs (*Heteroptera*) was classified as aphidophages. Two groups were taken into consideration.

Predatory: *Nabis pseudoferus* Rem., *N. ferus* L., *Himacerus apterus* F., *Orius niger* Wolff., and *Deraecoris ruber* L. The group of phyto-zoophags included eight species, among which *Lygus rugulipennis* Popp., and *L. pratensis* L. made up 93% of the individuals. The fact that these species feed on aphids is more and more widely accepted recently (Boness 1963, Strawiński 1964). Larvae of *Chrysopa* sp. occurred on the investigated fields in so small a number that they did not play any more significant part in the reduction processes of the Colorado beetle eggs.

The course of changes in numbers of aphidophages (Fig. 4) on the two fields had a similar character. Their appearance on both the fields commenced

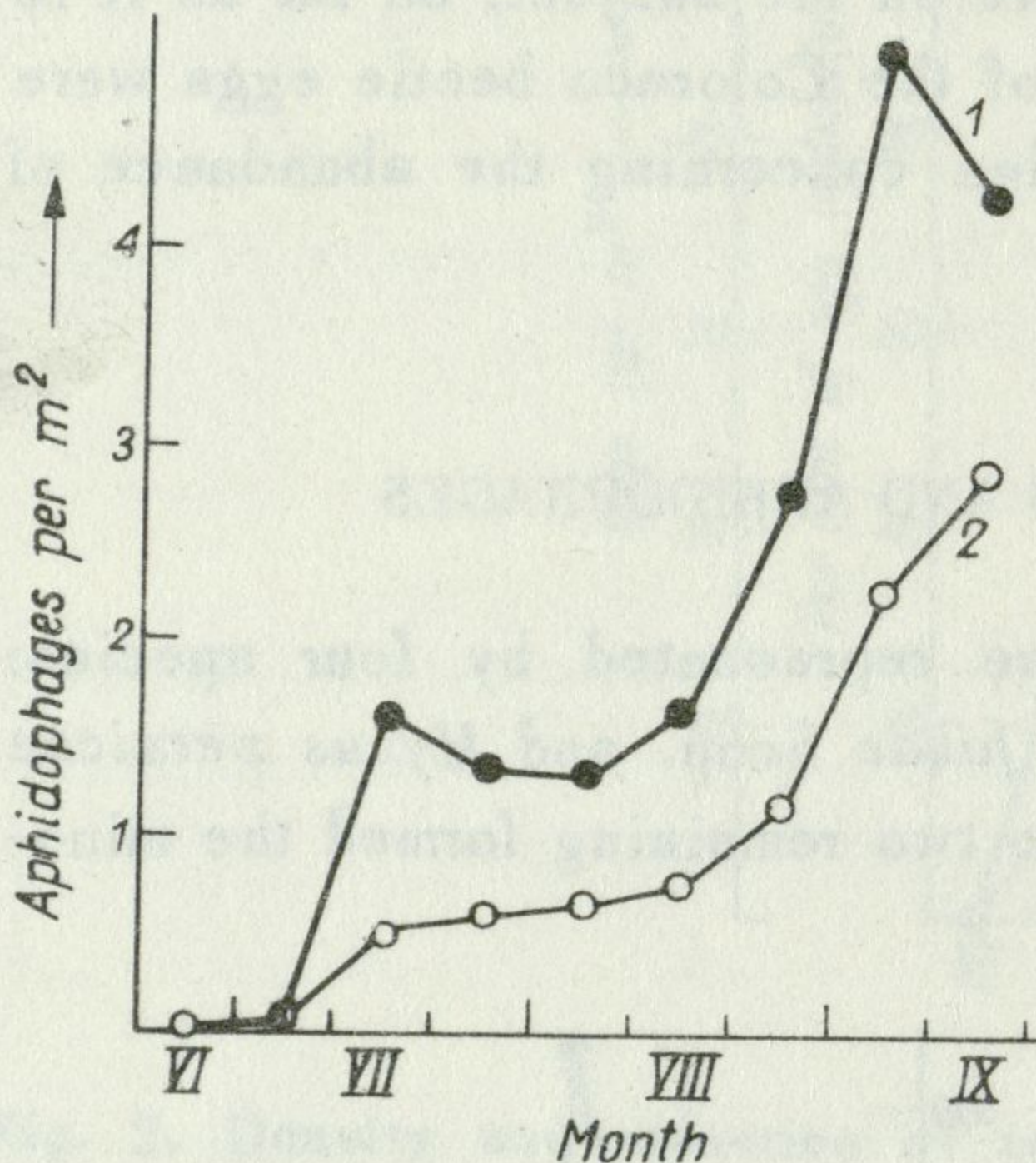


Fig. 4. Seasonal fluctuations in numbers of aphidophages in potato fields
1 — eastern field, 2 — western field

in the middle of July and until the middle of August the number of aphidophages remained on more or less the same level. Beginning from the second half of August a rapid increase in numbers of aphidophages was recorded on the two fields. On the eastern field the number of aphidophages was higher than on the western one. The most significant effect on the course of changes in numbers of aphidophages was exerted by bugs which particularly in the latter half of the summer dominated on the two potato fields. The most numerous were represented species from the genus *Lygus* whose mass appearance in autumn on the fields is a quite commonly observed phenomenon (Strawiński 1955) and most probably is connected with the fact that the potato field becomes more and more weed-grown just in this period.

ALIMENTARY CONDITIONS OF APHIDOPHAGES AND REDUCTION OF THE COLORADO BEETLE EGGS

The appearance of a new source of food in the biocenose may boost the interest of animals in it only in specified circumstances. This sort of food

should be equally attractive as the one that the given group of animals had been using up till then.

And here not always simple dependences were observed. No correlations between the egg reduction and either the number of aphids or aphidophages occurred in the analysed material. It must be pointed out here that the chemical composition of the Colorado beetle eggs considerably differed from the chemical composition of aphids, different were also stimuli sent by the aphids and by the Colorado beetle eggs. Undoubtedly aphidophages much better found out aphids in the field and most probably they preferred aphids to eggs of the Colorado beetle to which in view of the fact that they differ in taste aphidophages were not accustomed. Eggs of the Colorado beetle – a new sort of food introduced into the environment, and so they should attract less interest as far as aphidophages were concerned than aphids. This supposition was supported by the material. The attitude of aphidophages to eggs of the Colorado beetle was mainly conditioned by the alimentary resources of the environment (Fig. 5) that is the number of aphids. If there were more than 200 aphids per one aphidophage on the area of his penetration

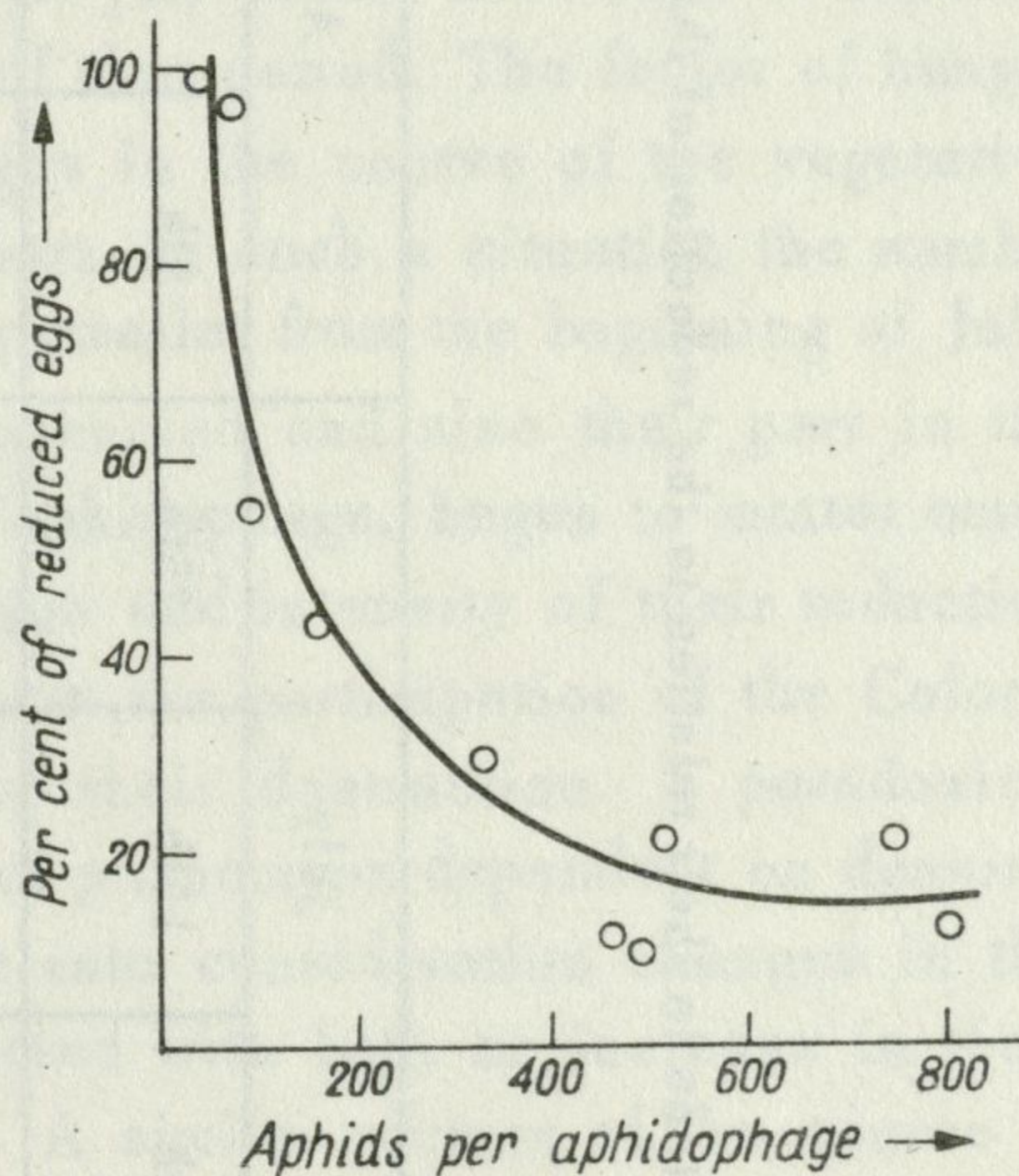


Fig. 5. Interrelation between quantity of food available for aphidophages and the reduction of the Colorado beetle eggs

the destruction of the Colorado beetle eggs was quite insignificant and it did not exceed 20% of the number of laid eggs. However in such cases when the density of aphids was low and there were less than 200 aphids per one aphidophage the per cent of destroyed eggs of the Colorado beetle increased. The phenomenon of the Colorado beetle reduction demonstrated a strong connection with the alimentary conditions of aphidophages. In the places where there were many aphids and an insignificant number of aphidophages the reduction of the Colorado beetle was low. When the number of available aphids was small aphidophages were hungry and in such a situation their interest in other kinds of food increased. This caused an increased reduction of the Colorado beetle eggs.

This phenomenon found its expression in the course of the reduction processes of the Colorado beetle (Tab. III). The first factor determining the situation in which the population of aphidophages occurs, may be described as changes in their densities and connected with that changes in the area pe-

Area occupied by individual aphidophages, its food contents in their relation to the reduction of the Colorado beetle eggs

Tab. III

		June	July			August			Sept.
		25th	5th	15th	25th	5th	15th	25th	5th
Area occupied by aphidophage (m ²)		—	12.5	2.04	1.75	1.54	1.33	0.88	0.45
Food available on the area	Aphids	—	5,490	463	794	519	335	176	47
	Eggs of Colorado beetle	172	564	52	42	11	3	1	0
	Total	172	6,054	515	836	530	338	177	47
	Per cent of eggs in the food of aphidophages	100	9.3	10.1	5.3	2.1	0.9	0.6	0.0
Per cent of reduced eggs		12.0	16.2	13.0	20.6	20.6	29.0	100.0	0.0

netrated by single individual. These changes of area, if we ignore here the beginning of July when the population of aphidophages only started to form on the two investigated fields and a single individuals fed on fifty potato plants, were nearly five-fold. In September, at the end of the vegetation of potatoes the area of penetration of on aphidophage included already only two potato plants. Changes in the area were particularly clearly reflected in the amount of available food. The number of aphids that can be found by an aphidophage on the area occupied by it fell from the end of July to the first days of September and it was 17-times smaller at the end of that period. The factor of hunger in the biocenose in the case of aphidophages in the course of the vegetative season of the potato played an increasing part. In such a situation the number of the Colorado beetle eggs, although getting smaller from the beginning of July, both as far as the absolute number was concerned and also their part in the food available on the area occupied by the aphidophage, began to matter much more. The changes in the participation of eggs and intensity of their reduction were quite striking (Tab. III). The smaller was the participation of the Colorado beetle, the higher was the per cent of their destruction. A paradoxical picture, when it is analysed in the category of phenomena dependent on density, becomes more understandable when we take into consideration changes in the alimentary situation of aphidophages connected with both an increase in their number and a drop in the number of aphids. A similar picture of the course of the analysed ecological phenomena was observed on both these potato fields.

The process of the biocenose adaptation to the species newly entering the area, as it was observed in the case of the Colorado beetle eggs, is conditioned by the existing ecological connections. Eggs of the Colorado beetle, as it was shown by numerous laboratory and field observations, may be destroyed by a group of aphidophages. The effectiveness of this biological group depends neither on the number of eggs of the Colorado beetle nor on the density of aphidophages. The number of aphids per one aphidophage is the main factor causing a change in the alimentary preferences of aphidophages and their shift to eggs of the Colorado beetle. When densities of aphids are low aphidophages because of hunger effectively destroy eggs of the Colorado beetle. When aphids are numerous on the area penetrated by aphidophages contacts aphidophage — eggs of the Colorado beetle are of an accidental character and contribute only in an insignificant degree to the destruction of eggs.

The above described situation corresponds to the present state of relations between three components: eggs of the Colorado beetle, aphids and aphidophages. And a question to be answered in future comes to the front whether the existing structure of relations will undergo changes and in what a degree. The

fact that aphidophages get used to eating eggs of the Colorado beetle, which occurs particularly clearly in autumn when they are in difficult alimentary conditions provides perspectives for their further adaptation to using those eggs as a source of food in other periods, particularly in summer, when density of eggs on potato plants is at its highest level.

CONCLUSIONS

1. Dependence of the reduction of the Colorado beetle eggs on their density is of an apparent character.
2. The reduction of the Colorado beetle eggs in the period of their highest density is the smallest and the most intensive reduction occurs in the period when the eggs are laid.
3. Aphidophages destroy eggs of the Colorado beetle only when the population of aphids undergoes liquidation and hunger forces aphidophages to look for other sources of food.
4. The biocenose of the potato field, without introducing alien species into it, shows elements which get used to treating eggs of the Colorado beetle as an alimentary basis in some special circumstances.

I desire to express my indebtedness to Dr. Barbara Gałęcka for supplying me with data concerning numbers of aphids and specific composition of lady-birds occurring in the investigated fields.

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REDUKCJA JAJ STONKI ZIEMNIACZANEJ (*LEPTINOTARSA DECEMLINEATA* SAY) JAKO ZJAWISKO ZALEŻNE OD GŁODU

Streszczenie

W trakcie badań nad redukcją naturalną jaj stonki na polach ziemniaczanych, nie objętych zwalczaniem chemicznym, stwierdzono paradoksalną z ekologicznego punktu widzenia sytuację: ilość zniszczonych jaj stonki przy dużych zagęszczeniach jest mniejsza (fig. 1) niż przy zagęszczeniach małych. Redukcja jaj stonki jest największa w sierpniu (fig. 2), pod koniec okresu rozrodu stonki. Stwierdzono brak korelacji redukcji jaj stonki z liczebnością afidofagów i mszyc (fig. 3, 4). Czynnikiem decydującym o niszczeniu jaj stonki są warunki pokarmowe afidofagów (fig. 5). Jeśli na jednego afidofaga przypada mniej niż 200 mszyc (tab. III) zwiększa się ilość zjadanych przez nie jaj stonki, mimo bardzo małego udziału jaj stonki w pokarmie afidofagów w tym okresie.

Zaobserwowane zależności pozwalają na umieszczenie jaj stonki w kompleksie ekologicznym mszyce-afidofagi, w którym rozmiary redukcji jaj stonki określają stosunki między dwoma głównymi komponentami. W okresie, w którym afidofagi mają dobre warunki pokarmowe, niszczenie jaj stonki zależy jedynie od przypadkowych kontaktów. W okresie złych warunków pokarmowych afidofagów, jaja stonki stają się pokarmem poszukiwanym. Sytuacja taka stwarza perspektywy dalszej adaptacji afidofagów do korzystania z jaj stonki jako źródła pokarmu, szczególnie w okresie największego zagęszczenia jaj.

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