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FLUCTUATIONS IN NUMBERS AND REDUCTION OF THE COLORADO  
BEETLE (*LEPTINOTARSA DECEMLINEATA* SAY)  
IN NATURAL CONDITIONS

The reduction in a population of the Colorado beetle (*Leptinotarsa decemlineata* Say) was investigated in natural conditions on the basis of the course of the fluctuation in numbers on two potato cultures excluded from the chemical control.

The natural reduction of the Colorado beetle larvae reaches 93% of the initial number of eggs. The intensity of reduction increases during the season. The reduction of larvae is directly proportional to their density and inversely proportional to the degree of aggregation.

The aim of the paper is to analyse the course of reduction of the Colorado beetle populations (*Leptinotarsa decemlineata* Say) in natural conditions. Fluctuation in numbers of the population and the way of its distribution in space have been taken as the background of the analysed phenomena. Field observations were carried out on potato cultures excluded from the chemical control.

The Colorado beetle covered in the post-war period the area of Poland and as a dangerous pest has been often taken as the subject of numerous papers. The invasion of this pest has not been checked so far and its populations are characterized by a considerable biotic potential. They cover potato plantations



and destroy, sometimes completely, the foliage of the plants. The long list of the enemies of the Colorado beetle (Bogdanov-Katkov 1947) did not reduce, in the least, its impact. The idea that the biocenose of the potato field is powerless against the pest, put forward in Poland by Węgorek (1959), has originated in this background. Scanty ecological material forming the basis of such considerations is surprising. Papers discussing various aspects of the biology, physiology, harmfulness and control of the Colorado beetle are very copious (Łarczenko 1957). Against the background of a considerable achievement of laboratory investigations on the Colorado beetle, exceptional insufficiency of ecological investigations is particularly striking. Papers giving information on the course of the fluctuations in numbers of the Colorado beetle and its reduction in natural conditions are very scanty.

Kaczmarek (1955) carried out experiments on a certain number of chosen plants of potato, artificially infected with the Colorado beetle eggs. He investigated the reduction by censusing individual larval stages of these plants. On the basis of the obtained results he developed the idea of the natural reduction of the Colorado beetle in connection with density dependent phenomena.

Franz (1957) stressed the fact that the degree of the Colorado beetle reduction depends on various groups of predators and parasites. His experiments were carried out on individual plants of potato, mainly under isolators. Both the above mentioned authors recorded a considerable reduction of the Colorado beetle population in natural conditions.

Besides these investigations on the Colorado beetle reduction, numerous observations were carried out on its real and potential enemies. Together with some additions offered by Węgorek (1959) the list of such enemies is of a considerable length. However, investigations concerned with the efficiency of individual species in the biocenoses of cultivated potatoes plantations do not give so clear-cut results as cultures realized in laboratories, and the obtained results, mainly on account of the defects of the applied methods, are not constructive in any estimate of the size of the Colorado beetle populations reductions in nature. The significance of the problem to the economy induced us to take up investigations which would enable to give a rough estimate of the intensity of the Colorado beetle reduction in nature without taking into consideration weak sides of other methods, such as chosen plants or isolators.

#### AREA, METHODS AND MATERIAL

The investigations were carried out in 1965 in two one-hectare potato fields which are part of the area of the State Farm Rogaczewo in district Kościan. These fields are situated as a part of the eight-hectare experimental



area on which cultures were grown according to a permanent crop-rotation. Parallel microclimatic investigations were carried out in these fields. The two fields were separated from each other by a shelterbelt, consisting mainly of *Robinia pseudacacia*, pointing in the N-S direction. Its width amounts to 36 m and its height to 15 m. The fields were of a rectangular shape with the dimensions of 250 m by 40 m and their shorter sides were adjacent to the shelterbelt. In the vicinity of the fields there were rye fields on the northern side and barley fields on their southern side. The western field on the western side was next to a field of maize, while the eastern one was adjacent on the eastern side to a pea plot. The soil of the two fields consists of an average sand on clay. The fertilization and previous crop-rotation were unchanged. Rye was sown as a fore-crop. Potatoes of the „Lenino” variety, ordered from Pomorze in 1963, were used as seminal material. 30 quintals per hectare were sown. The same kind of agrotechnics was applied to the fields and after the rye had been gathered in, the first ploughing was carried out in the 31st July, 1964, while harrowing was on the 6th August of the same year. 150 quintals per hectare of cow dung was supplied to the fields and then ploughed 18 cm deep on the 20th May, 1965, and the field was harrowed. Fertilization was carried out on the 21st May, 1965. The following fertilizers were used then:

40% potassium salt	250 kg/ha,
18% superphosphate	300 kg/ha,
20% ammonium sulphate	200 kg/ha.

The planter applied had the gap of 62 cm. After the potatoes had been planted the field was earthed up on the 25th May, 1965. On the 4th and 5th June, 1965, the field was earthed up and harrowed, and on the 19th June, 1965, it was weeded out with the help of drill hoe. The next earthing up and fertilization with ammonium sulphate, of which the amount of 100 kg/ha was taken, was carried out on the 7th July, 1965. The manual weeding of the field was carried out between the 8th and 13th of July, 1965. The last earthing up was carried out on the 14th July, 1965. The potatoes sprouted in the last days of May, digging was carried out on the 23rd September, 1965. Chemical control was not applied.

The vegetative season of 1965 was relatively cool and wet (Tab. I) as compared with the average conditions.

Investigations on the abundance of the Colorado beetle were carried out from 19th June to 23rd September, 1965. The information was collected in the following way. A quantitative sample consisted of eggs, larvae and adult individuals of the Colorado beetle occurring at the time on a single potato plant.



Monthly average extremal temperatures and precipitation on the experimental fields

Tab. I

Microclimate factor		Year	Month				
			V	VI	VII	VIII	IX
Temperature	maximal	1965	16.7	24.3	23.9	24.6	22.3
		1953-1964	19.7	25.1	26.5	24.9	21.0
	minimal	1965	4.3	10.2	10.9	8.6	7.7
		1953-1964	6.1	9.7	11.5	11.1	7.9
Precipitation		1965	95.4	80.5	133.0	14.3	38.3
		1953-1964	48.3	48.9	64.8	70.2	44.3

A series of samples consisted of 120 plants. The person doing the collecting covered the field in a zig-zag way. The first potato plant was chosen at random near the edge of the field, and each next sample was taken at a distance of five plants from the previous one, and only rows were changed because then the interval consisted of an even number of plants when moving in one direction, or of an odd number of plants when coming back after reaching the opposite end of the field. Owing to the application of this method the whole field was more or less evenly covered with a net of samples. The adult beetles and larvae of all the stages were counted on the spot by looking through the leaves of potatoes. Egg layers were collected together with the leaves on which they were laid, and the number of the eggs was estimated in the laboratory, and besides dividing them into damaged and not damaged. When the adult individuals were considered, the number of hibernating and new beetles were estimated separately and the beetles were classified into males and females. The samples were taken every three days. All in all 25,451 larvae, 12,011 adult beetles and 27,368 eggs were recorded on the two fields in the period of the investigations (Tab. II).

Comparison of material

Tab. II

Field	Total number of eggs	Destroyed eggs	Adults				Larvae			
			1-th generation		2-nd generation		L <sub>1</sub>	L <sub>2</sub>	L <sub>3</sub>	L <sub>4</sub>
			♂♂	♀♀	♂♂	♀♀				
Western	13,682	1,161	60	128	975	4,155	1,318	1,729	2,561	5,058
Eastern	13,686	1,369	66	144	1,285	5,198	1,558	2,301	3,741	7,185
Total	27,368	2,530	126	272	2,260	9,353	2,876	4,030	6,302	12,243



The estimate of the reduction. Starting from the 20th of July larvae of the fourth instar ( $L_4$ ) dominated on the two fields, while the younger development stages, particularly  $L_1$ , were only represented by a very small number of individuals. The recorded predominance, in numbers, of older larvae, may be caused by differences in the duration of individual development stages. The longer the given stage lasts, the more numerous it is in the collected material. The actual preponderance of the number of older larvae has a considerable bearing on the estimation of the intensity of feeding by the Colorado beetle on potato leaves.

In order to estimate the reduction of the Colorado beetle in the investigated potato cultures data concerning the number were recalculated to more comparable values by dividing them by the time each phase lasted. It enabled to set out the data which gave information on those individuals which hatched from eggs laid in different periods and in this way analyse the reduction of the Colorado beetle in natural conditions and in a developing population which is in complete, undisturbed contact with the biocenose. In our investigations any factors blurring the picture of the observed relations, as for example predominance of emigration over immigration which may take place in the case of experiments set up on single plants (Kaczmarek 1955) or a change of environment conditions and contacts with the biocenose caused by the application of isolators (Franz 1957) were eliminated.

Data concerning the duration of individual development stages were obtained by way of observations, carried out both in the laboratory and in field conditions on the isolated potato plants. The mean stage duration obtained on the basis of field observations amounted for eggs to 9 days, for  $L_1$  to 3,  $L_2$  to 5,  $L_3$  to 9,  $L_4$  to 15 days. Figures obtained in the laboratory breeding were much lower on the account of more favourable thermic conditions for the development of larvae. The time needed for the development of Colorado beetle in the field as compared with the data obtained by others (Węgorzek 1959) was somewhat longer. This difference may have been caused by an unusually cool summer (Tab. I).

#### FLUCTUATIONS IN NUMBERS

Imagoes. Beetles of the winter generation started swarming in 1965 on 13th–14th June in fields lying 3 km from the experimental areas on which the spring invasion of the Colorado beetle commenced with a week's delay (19th June) when the potatoes began to shoot up. The course of the changes in numbers of these beetles on both the fields may be divided into two periods (Fig. 1). The first of the two is somewhat longer (19th June–15th July) and is charac-



terized by a permanent low level of the number of beetles which amounts on the average to 0.26 individuals per 1 m<sup>2</sup>. The other period is characterized by changes in numbers, initially an increase which leads to a more intensive density of beetles, up to 0.56 individuals per 1 m<sup>2</sup> on 22nd of July in the eastern field. In the third part of July there came a sudden fall in the number of beetles from the winter generation. The last alive individuals belonging to this group were recorded dead on 30th August, lying on the ground still in September.

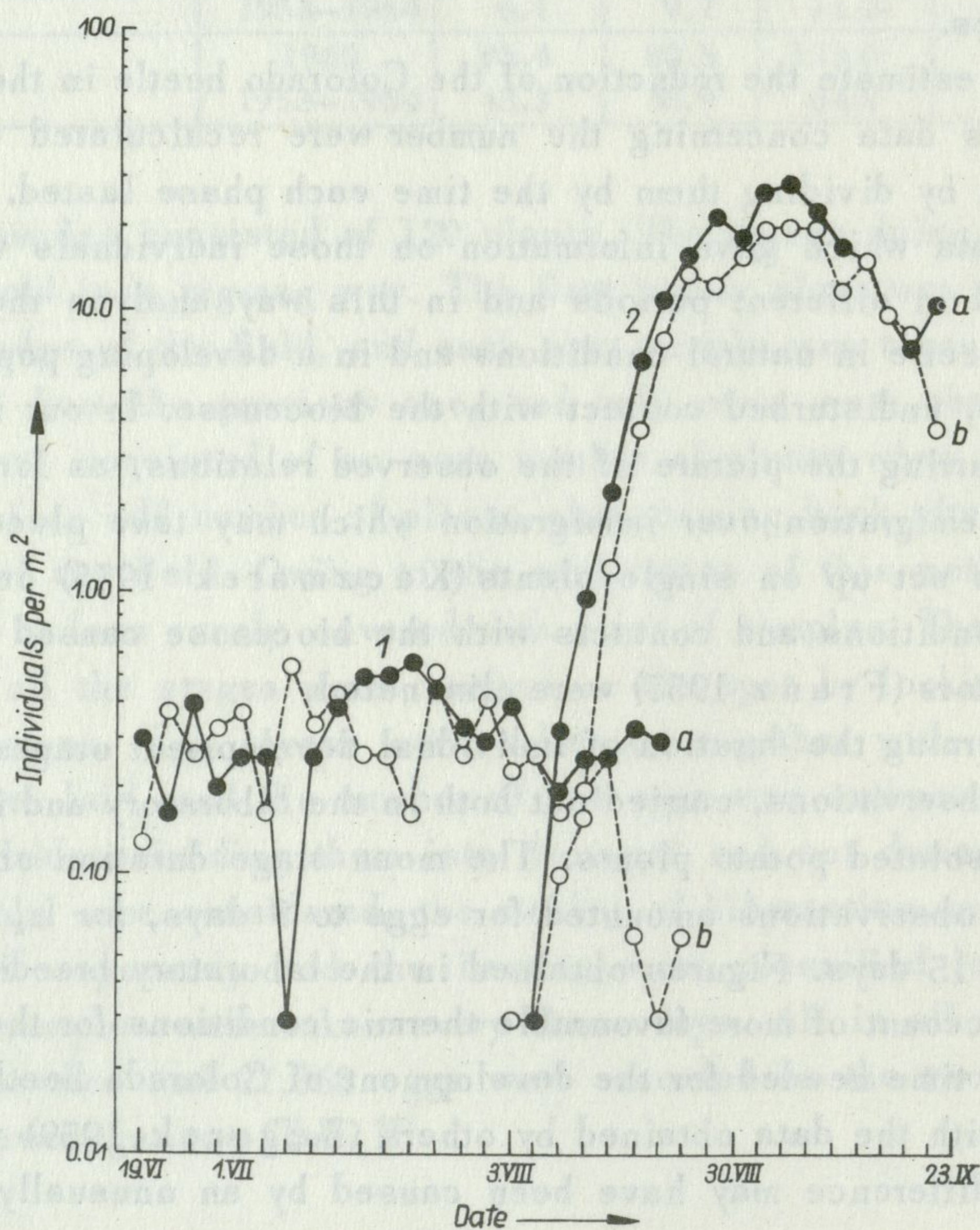


Fig. 1. Fluctuations in numbers of adult Colorado beetles on the two potato fields  
1 - hibernating generation, 2 - summer generation, a - eastern field, b - western field

First imagoes of the summer generation appeared at the beginning of August. Initially their density oscillated from 0.5 to 1.0 individual per 1 m<sup>2</sup>. However since the middle of August the number of individuals from this generation had been increasing rapidly. The highest number (29.10 individuals per 1 m<sup>2</sup>) was recorded on 5th September in the eastern field. Since that day till the digging started the number of imagoes from the summer generation to decrease, reaching in the final phase 2.29 individuals per 1 m<sup>2</sup>.



An insignificant number of imagoes from this generation was found a few days after the potatoes had been yielded.

These two generations of imagoes are characterized by a greater number of females as compared with males (Tab. III). The greater number of females from the winter generation is twofold and ones from the summer generation even fourfold, and this may indicate that the winter reduction of the Colorado beetle in the case of females is more intensive than in the case of males.

Sex relations of the Colorado beetles (per cent)

Tab. III

Generation	♀♀	♂♂
Hibernating	68.34	31.66
Summer	80.54	19.46

Eggs. The laying of eggs by insects belonging to the winter generation commenced at the same time when the beetles started swarming on 19th June. The initial density of eggs amounted to 7.43 eggs per 1 m<sup>2</sup>, but at the end of June reached up to 30.67 eggs per 1 m<sup>2</sup>. Till 10th July the highest number of laid eggs was recorded in both the fields (Fig. 2). In this period there occurred on the average 11.47 eggs on a single potato plant. But starting from 20th July the number of laid eggs decreased but considerable leaps were recorded and the process of egg laying became irregular. The appearance of imagoes belonging to the summer generation in the middle of August did not cause any increase in the number of laid eggs as in 1965 the summer generation did not reproduce. The whole development of the population of the Colorado beetle in the investigated fields must be attributed to the first winter generation of the Colorado beetle.

There were about 30–40 eggs in an egg-layer. More numerous layers were quite exceptional, i.e. those which consisted of a hundred or more eggs. All the layers may be divided into two categories: compact and dispersed. Compact layers consist of eggs adjoining to each other closely in regular rows. Dispersed layers are scattered irregularly all over the surface of the leaf. Both these types of layers were represented in the material in more or less the same degree.

After adding up the number of eggs and checking it with the comparable number by dividing by the time of its development we arrived at the total number of eggs laid by the Colorado beetle. It amounts to 304.08 eggs per 1 m<sup>2</sup> and 76.02 eggs per a single potato plant. If we take it that the number of females from the winter generation is equal to their highest density recorded



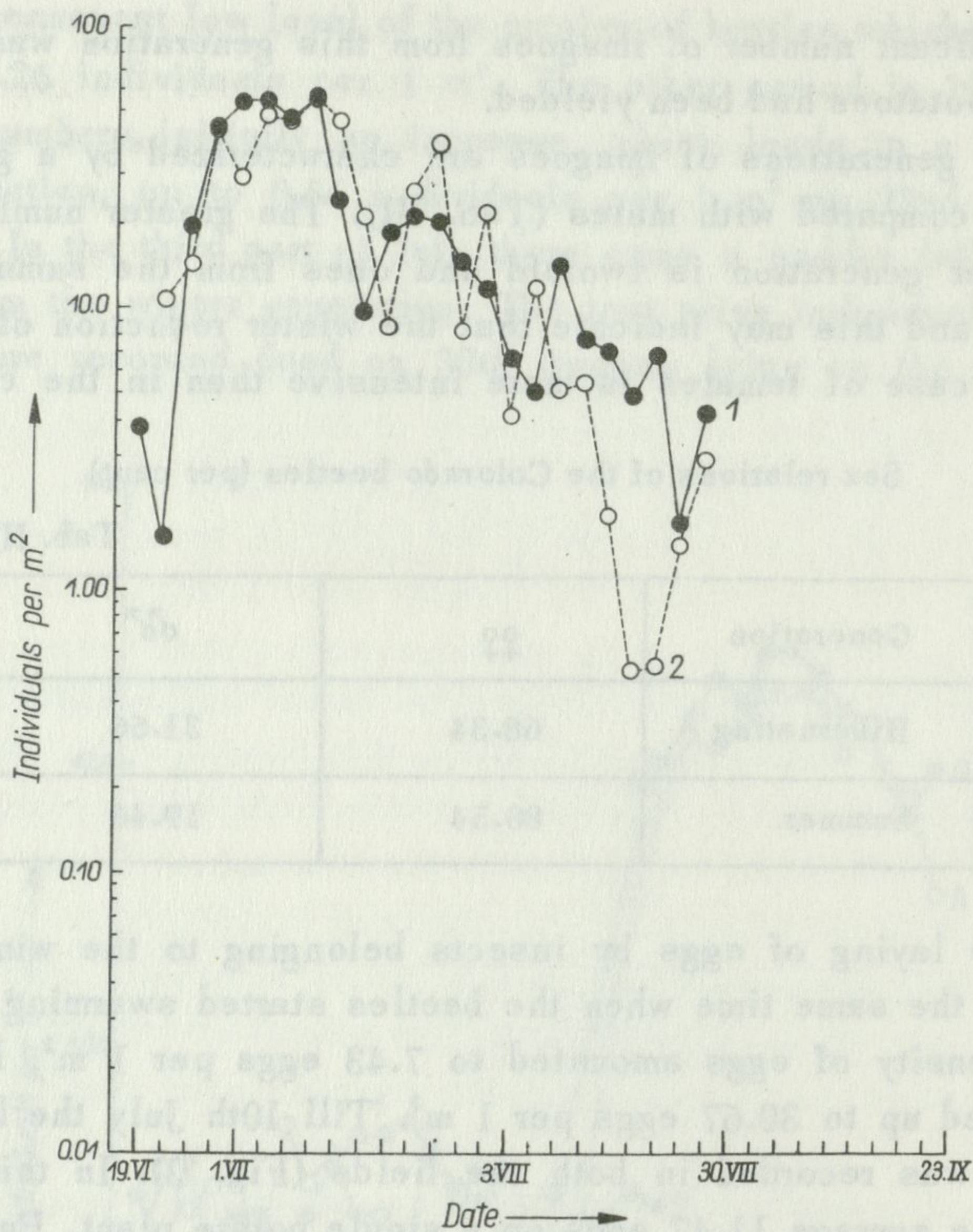


Fig. 2. Fluctuations in numbers of eggs laid by the Colorado beetle  
1 - eastern field, 2 - western field

at the end of the period of spring migration and amounts to 0.43 individuals per  $1 \text{ m}^2$  and if any further changes in numbers correspond only to the reduction of this figure, then the total sum of eggs laid by females in field conditions amounts to 707.2. This figure is considerably lower than the ones quoted by other authors (Węgorzek 1959, 1965) whose data based on laboratory observations correspond in a more significant degree to the possibilities of the investigated animals than to the realized fertility in concrete ecological conditions. Beside less favourable ecological conditions, in natural conditions we must take into account the reduction of females of the Colorado beetle which is most certainly a significant factor limiting the real number of eggs. Potential abilities of individuals in the case of the Colorado beetle are not realized in field conditions.

First instar larvae ( $L_1$ ) appear at the end of June (26th June), i.e. exactly nine days after first egg layers had been recorded. The appearance of these larvae has a different course in both the fields. In the western field the main



wave of the appearance of  $L_1$  falls on the first twenty days of July (Fig. 3). In this period this stage is dominant on potato fields. The highest number of  $L_1$  reaches up to 5.93 individuals per  $1 \text{ m}^2$ . In the course of the next month (25th July–24th August) the average number of  $L_1$  is low and shows three insignificant peaks. From the end of August first instar larvae appear only sporadically in the investigated field.

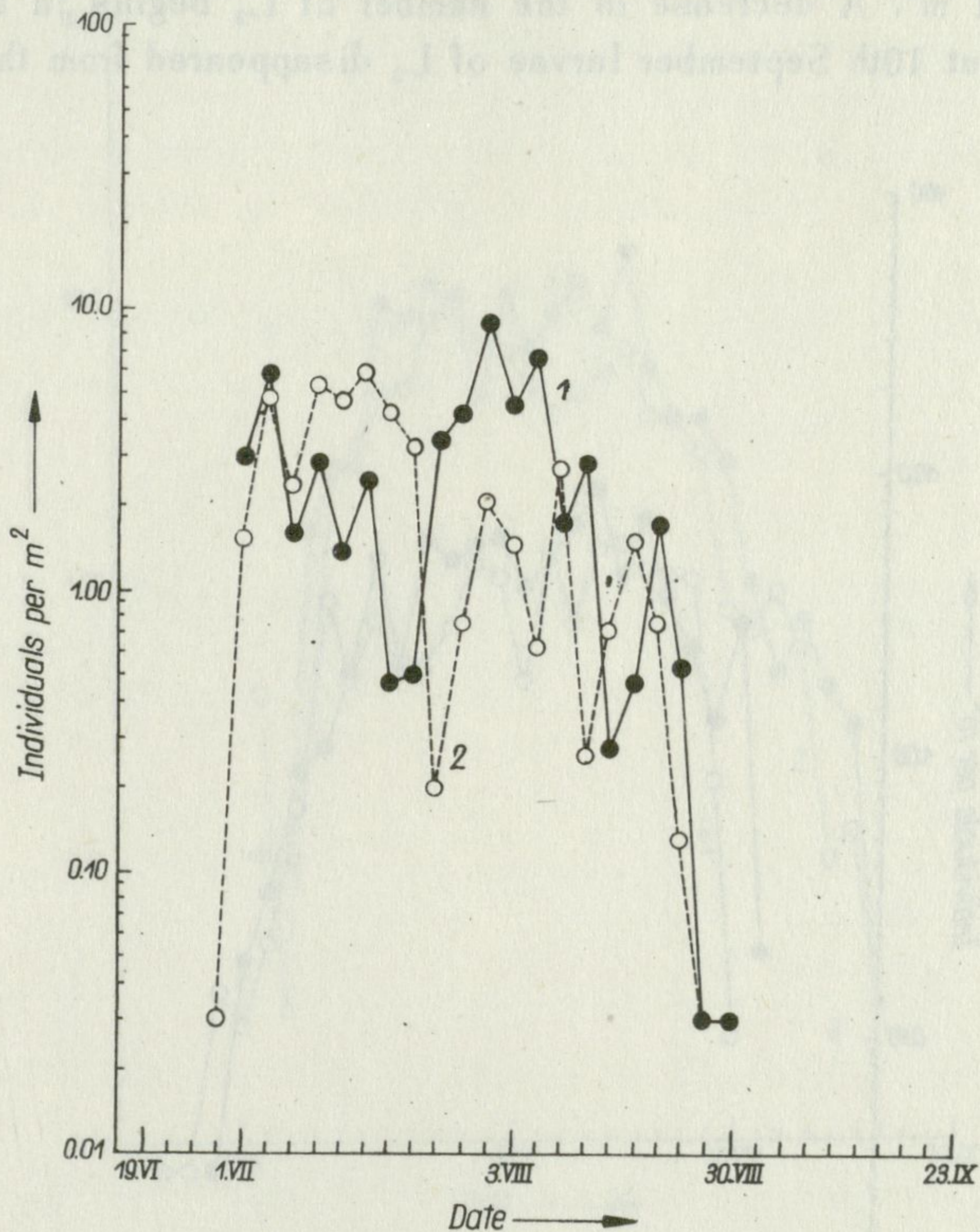


Fig. 3. Fluctuations in numbers of the first instar larvae of the Colorado beetle  
1 – eastern field, 2 – western field

In the eastern field the first wave of the appearance of  $L_1$  starts at the beginning of July but lasts only two weeks. The average density of larvae in this period amounts to 2.84 individuals per  $1 \text{ m}^2$  and is about twice lower than in the western field. On the other hand the second wave of the appearance of  $L_1$  (25th July–9th August) is bigger than the previous one. The highest density now reaches up to 8.9 individuals per  $1 \text{ m}^2$ . From about 10th August the abundance of  $L_1$  on this field decreases and similarly as in the western field no further appearances of this instar were recorded till the end of the month.



Second instar larvae ( $L_2$ ). The appearance of  $L_2$  in the western field shows some delay as compared with  $L_1$  connected with the larval development. An increase in numbers of  $L_2$  was recorded in this field between 13th and 19th July. Until 6th August the number of  $L_2$  was more or less stable with the density of 4.12 individuals per  $1 \text{ m}^2$  showing however some fluctuations (Fig. 4). In August the density of  $L_2$  remained on a considerably high level – 1.88 individuals per  $1 \text{ m}^2$ . A decrease in the number of  $L_2$  begins in the last days of August. About 10th September larvae of  $L_2$  disappeared from this field completely.

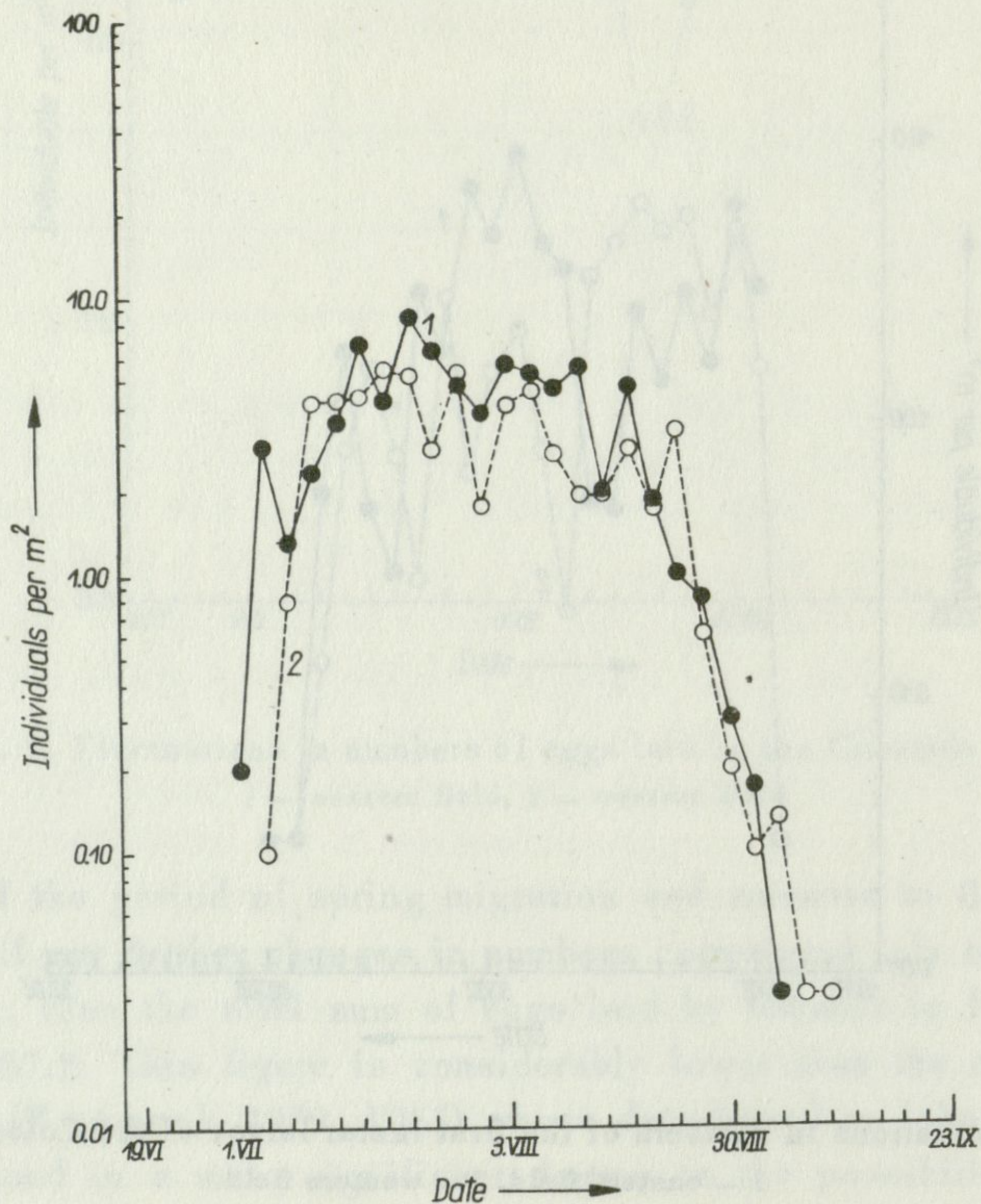


Fig. 4. Fluctuations in numbers of the second instar larvae of the Colorado beetle  
1 – eastern field, 2 – western field

In the eastern field the initial appearance of  $L_2$  is simultaneous with the appearance of  $L_1$  and has a similar course. About 20th July the highest number of  $L_2$  – 8.5 individuals per  $1 \text{ m}^2$  – was recorded and then the number decreased showing at times considerable fluctuations (Fig. 4). The appearance of larvae of  $L_2$  terminated in this field earlier than in the eastern one. The last individuals of  $L_2$  were recorded here on 2nd September.



In the eastern field the initial appearance of  $L_2$  is simultaneous with the appearance of  $L_1$  and has a similar course. About 20th July the highest number of  $L_2$  – 8.5 individuals per  $1\text{ m}^2$  – was recorded and then the number decreased showing at times considerable fluctuations (Fig. 4). The appearance of larvae of  $L_2$  terminated in this field earlier than in the eastern one. The last individuals of  $L_2$  were recorded here on 2nd September.

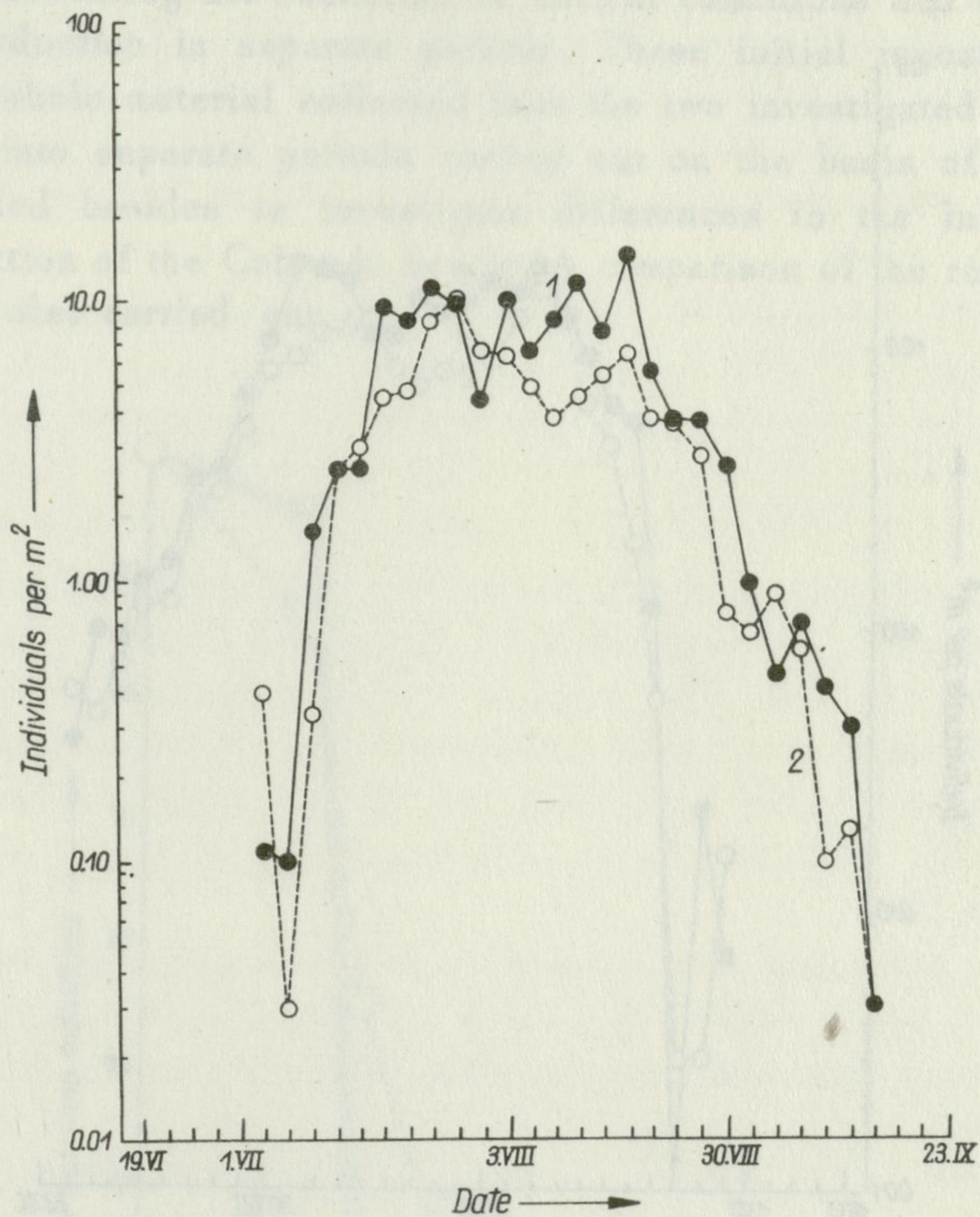


Fig. 5. Fluctuations in numbers of the third instar larvae of the Colorado beetle  
1 – eastern field, 2 – western field

Third instar larvae ( $L_3$ ). The course of the appearance in the two plantations was very similar and this makes it possible to discuss the two variants together. The appearance of  $L_3$  commenced at the beginning of July. The first peak (Fig. 5) was clearly seen about 25th of July. Then  $L_3$  reached the density of 10.2 individuals per  $1\text{ m}^2$ . After that a decrease in the number of  $L_3$  was recorded which in the eastern field was delayed till the end of July and in the western one till about 10th August. The second peak of  $L_3$  fell on the middle of August; in the eastern field it was higher than the first peak – 14.37 indivi-



duals per 1 m<sup>2</sup>, and in the western field somewhat lower than the first peak – 6.30 individuals per 1 m<sup>2</sup>. Since then a decrease in numbers of L<sub>3</sub> had been recorded. The last larvae of L<sub>3</sub> were recorded on 20th August.

Fourth instar larvae (L<sub>4</sub>). First individuals appeared on 4th July, however the wave of the appearance commenced only on 10th July. The course of changes in numbers in the two fields was similar as in the case of L<sub>3</sub> (Fig. 6). In the

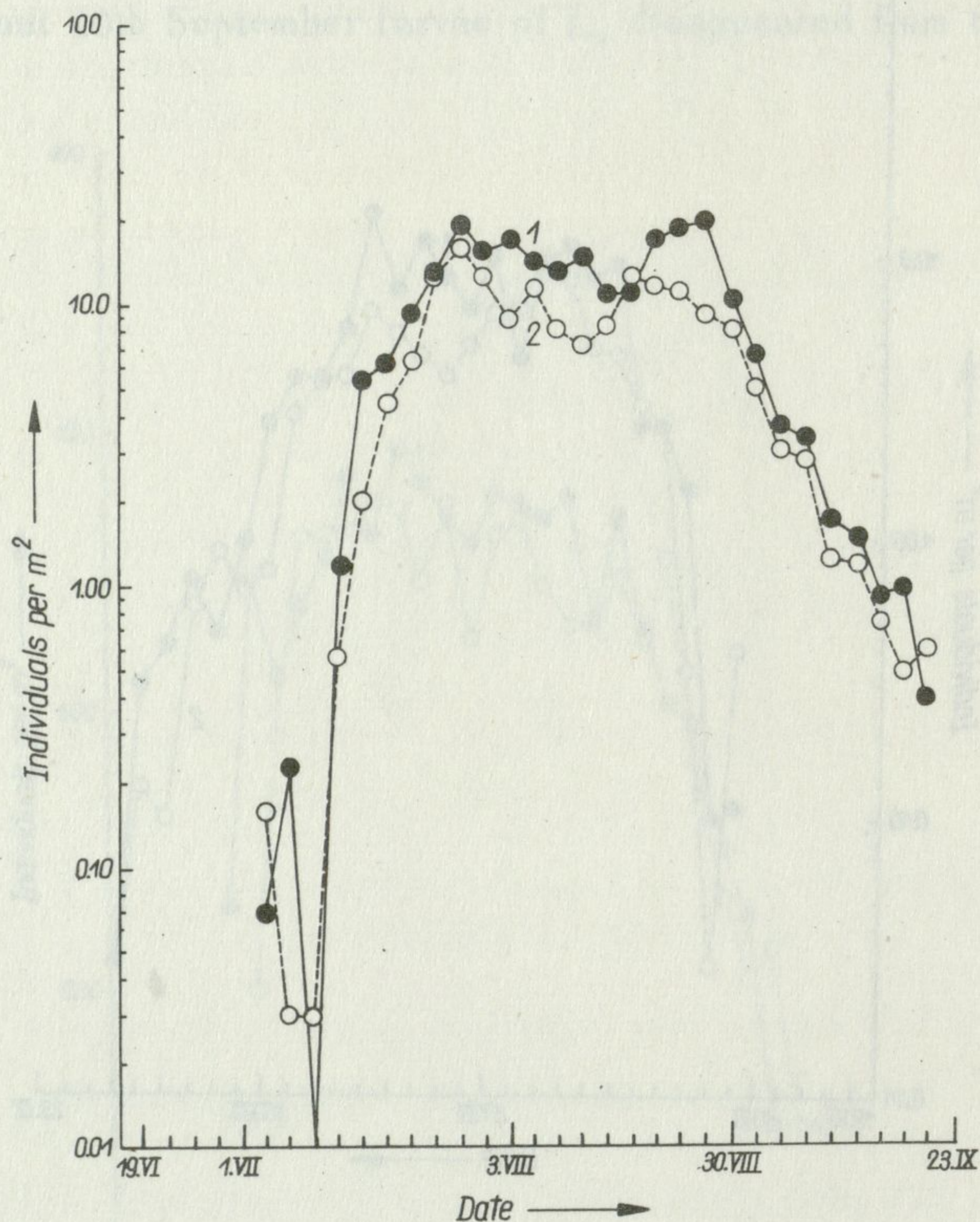


Fig. 6. Fluctuations in numbers of the fourth instar larvae of the Colorado beetle  
1 – eastern field, 2 – western field

western field the delay in the appearance of L<sub>4</sub> as compared with L<sub>3</sub> was insignificant. In the eastern field the delay, particularly of the second peak, amounted to nine days. The number of L<sub>4</sub> in view of the time needed for this stage is higher than in the case of larvae from the previous development stages. In the western field the highest number of L<sub>4</sub> fell on the end of July and amounted to 16.17 individuals per 1 m<sup>2</sup>. In the eastern field the peak that occurred in the third and last part of July – 19.40 individuals per 1 m<sup>2</sup> – was only a little lower than in the third and last part of August – 20.13 individuals per 1 m<sup>2</sup>. Larvae of L<sub>4</sub> remained in both these fields until the digging of potatoes.



THE REDUCTION OF THE COLORADO BEETLE IN NATURAL CONDITIONS

In his investigations on the course of the reduction of the Colorado beetle Kaczmarek (1955) and Franz (1957) take into account first of all the size of the reduction of the Colorado beetle in various experimental conditions. The technique applied in our investigations enabled to analyse general character of the curve presenting the reduction in natural conditions and an estimate of the rate of reduction in separate periods. These initial investigations were based on the whole material collected from the two investigated potato fields. The division into separate periods carried out on the basis of the collected material enabled besides to investigate differences in the intensity of the seasonal reduction of the Colorado beetle. A comparison of the reduction in the two fields was also carried out.

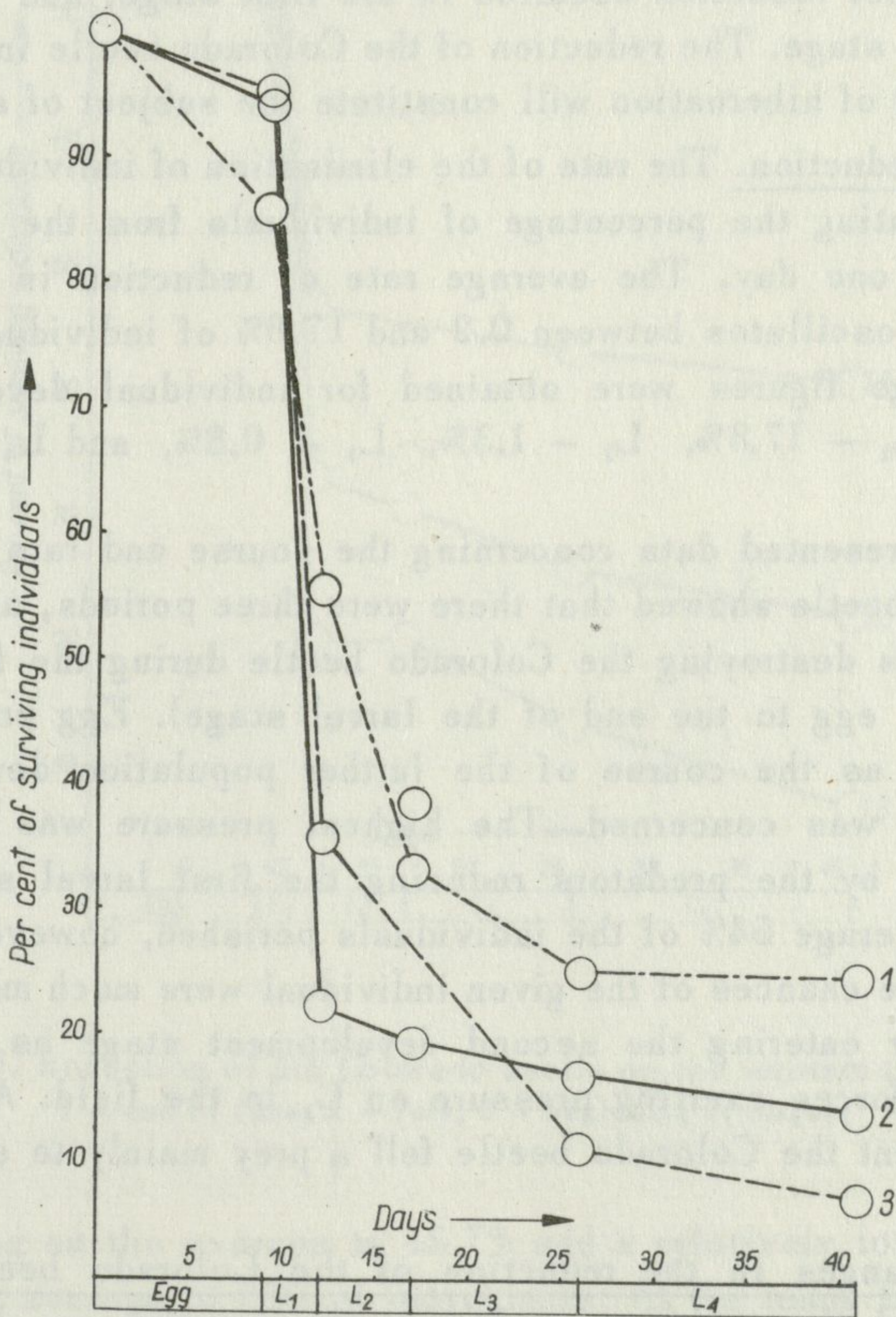


Fig. 7. Reduction of Colorado beetle on the eastern potato field  
 1 - end of June, 2 - July, 3 - beginning of August



The course of the reduction (Fig. 7). The curve presenting the reduction of the Colorado beetle population in each of the investigated by us cases had a similar character and the shape of letter "L". Such a course of the curve may have been caused by an uneven intensity of the reduction of the Colorado beetle in individual development stages. The reduction of eggs oscillated between 5% and 18.5% and as compared with the next period was relatively low. The highest reduction of the Colorado beetle occurred in  $L_1$  and amounted to 30–72% of the number of laid eggs. In the first three days of the development we observed the greatest drop in numbers. In  $L_2$  the size of the elimination was considerably smaller than in  $L_1$  and it amounted to 0–22.5%. In the third stage the reduction kept decreasing (2.5–16.5%) and in the last stage ( $L_4$ ) it amounted to 0.5–6.5%.

The average reduction in individual development stages presented itself as follows: eggs – 11.2%,  $L_1$  – 53.6%,  $L_2$  – 6.7%,  $L_3$  – 6.9%,  $L_4$  – 3.3%. Clearly the highest reduction occurred in the first stage, and the smallest one in the last larval stage. The reduction of the Colorado beetle in the pupal phase and in the period of hibernation will constitute the subject of a separate paper.

The rate of reduction. The rate of the elimination of individuals was investigated by calculating the percentage of individuals from the given stage that perished during one day. The average rate of reduction in the case of the Colorado beetle oscillates between 0.2 and 17.8% of individuals per day. The following average figures were obtained for individual development stages: eggs – 1.2%,  $L_1$  – 17.8%,  $L_2$  – 1.3%,  $L_3$  – 0.8%, and  $L_4$  – 0.2% of individuals per day.

The above presented data concerning the course and rate of the reduction of the Colorado beetle showed that there were three periods, and most probably also three groups destroying the Colorado beetle during the first development period (from the egg to the end of the larval stage). Egg predators were not decisive as far as the course of the further population development of the Colorado beetle was concerned. The highest pressure was rendered on the Colorado beetle by the predators reducing the first larval stage, as in this period on the average 54% of the individuals perished, however after surviving this stage the life chances of the given individual were much more considerable. The larvae after entering the second development stage as if escaped from the eliminating forces exerting pressure on  $L_1$  in the field. At the end of the larval development the Colorado beetle fell a prey mainly to amphibia (Mazur 1966).

Seasonal changes in the reduction of the Colorado beetle. In order to estimate seasonal changes in the reduction the material was divided into three periods. The first period included the individuals that hatched from eggs laid in the last ten days of June, i.e. in the period of increase in egg density. The second period – July includes the peak in the density of eggs on both the



investigated fields and the beginning of the phase when a decrease in numbers of eggs was recorded. The third period – the first ten days of August includes the phase of the decrease and low number of eggs. The larvae hatched from eggs which were laid later was not considered. These larvae had not enough time for the complete metamorphosis and were destroyed during the digging.

The reduction of June layers (Fig. 8) was characterized by the elimination

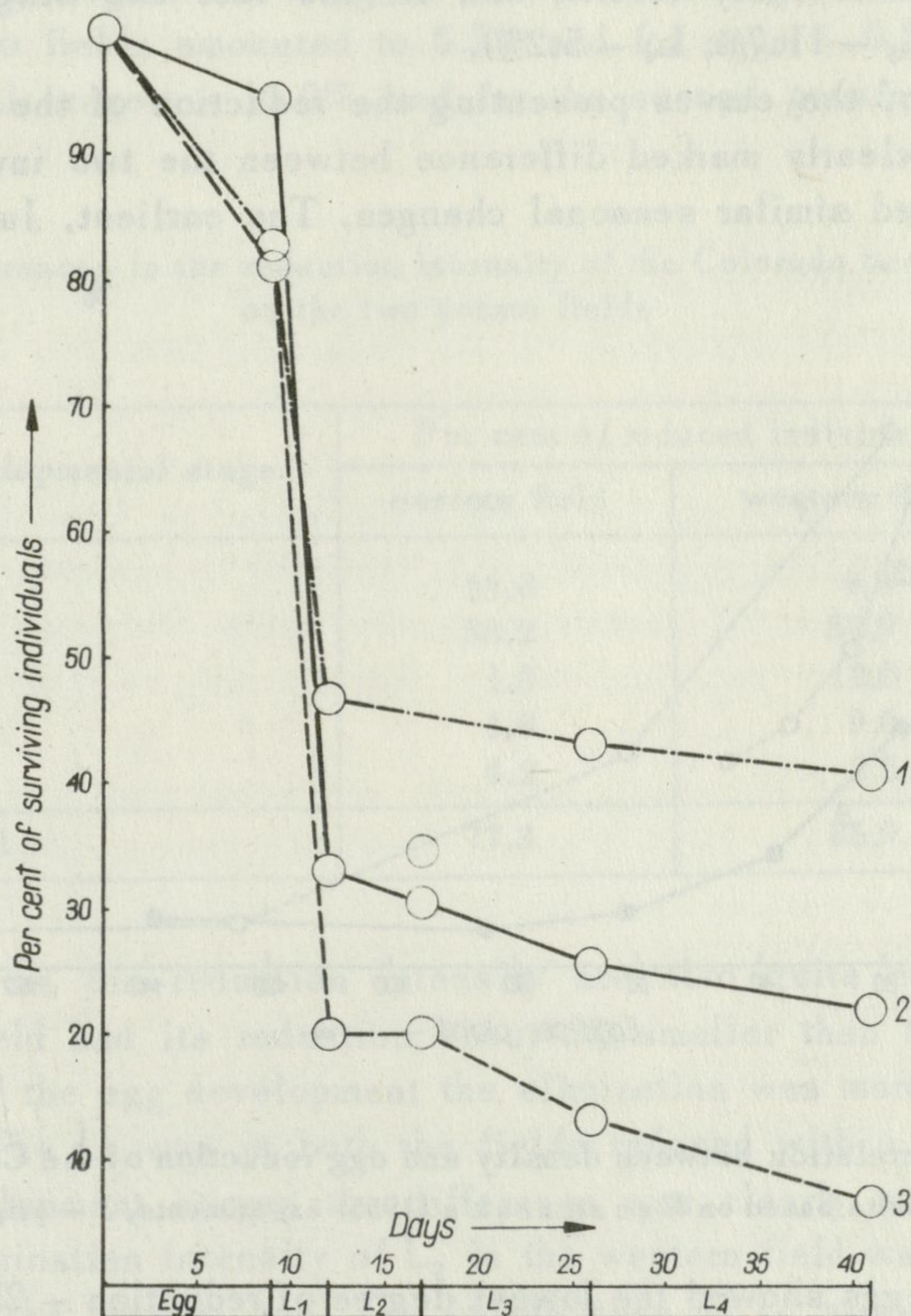


Fig. 8. Reduction of the Colorado beetle on the western potato field  
1 – end of June, 2 – July, 3 – beginning of August

of eggs amounting on the average to 15.7% and a relatively low reduction of  $L_1$  amounting on the average to 33% of individuals. At the same time the reduction of  $L_2$  amounted in this period to 12%, and this was relatively high for the given stage. On the other hand the two last development stages ( $L_3$  – 5.2%,  $L_4$  – 1.5% of individuals) were characterized by the reduction lower than the average one.



The reduction of eggs from the July layers had a different character. The percentage of destroyed egg layers (6.0%) was considerably lower than the average and the intensity of reduction of  $L_1$  – 66.5% – reached the highest level. In the last three larval stages ( $L_2$ – $L_4$ ) there also occurred some intensity in the reduction (2.7–3.7%) – smaller than the average.

The reduction of eggs from the August layers had its intensity near to the average (11.7%), the elimination of  $L_1$  (61.2%) was high and the reduction of  $L_2$  increased considerably (5.2%), and for the last two stages assumed the highest values ( $L_3$  – 11.7%,  $L_4$  – 5.2%).

The course of the curves presenting the reduction of the Colorado beetle in spite of the clearly marked difference between the two investigated fields (Fig. 8–9) showed similar seasonal changes. The earliest, June layers of the

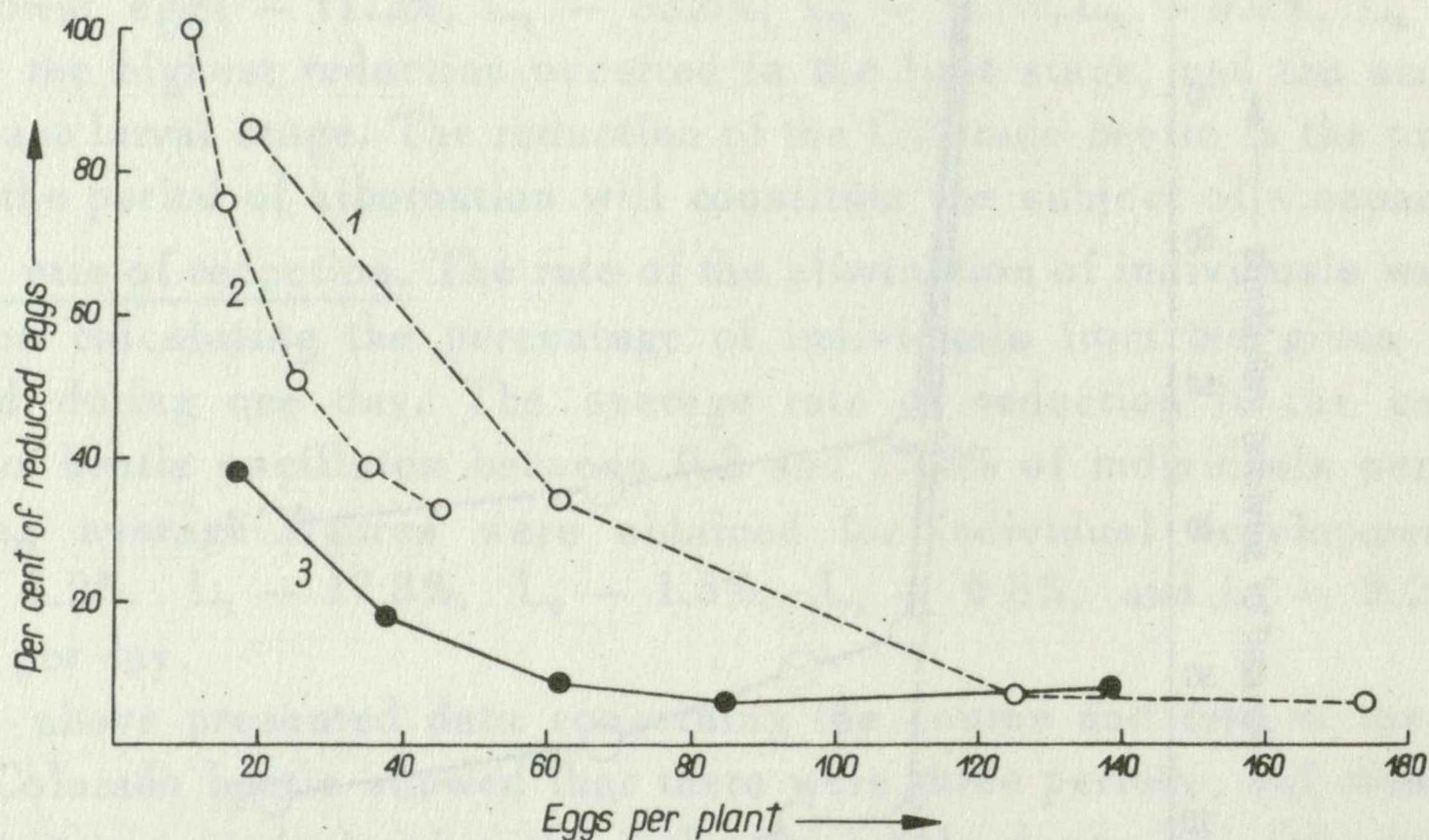


Fig. 9. The correlation between density and egg reduction of the Colorado beetle  
1, 2 – results based on Kaczmarek's (1955) experiments, 3 – original data

Colorado beetle eggs showed the lowest degree of reduction – 25–40% of individuals from these layers managed to survive, while from the July layers only 14–22% of individuals survived and from the August layers as little as 7%. These data make it possible to state that reduction of the Colorado beetle increases with time. The biocenose of the potato field adapts itself during the vegetative season to make use of the Colorado beetle as an alimentary basis.

Differences in the reduction of the Colorado beetle in the two fields. The number of beetles from the winter generation initiating development of the Colorado beetle population in the two fields was similar, and the number of eggs laid by them nearly identical. In the two fields the same crop rotation



was applied, and soil and microclimatic conditions were also very similar. The recorded differences in numbers of larvae and the course of the reduction may be mainly attributed to the dissimilarity of the biocenotic factors of the two investigated fields.

Differences in numbers were clearly seen only in the case of larvae. The eastern field was characterized by a greater number of larvae from all the stages. This difference was already distinct in the case of  $L_1$ , and it increased for the remaining stages. For imagoes from the winter generation the difference between the two fields amounted to 5.5% and for eggs – 0.01%, for the total of all the larval stages – 16.2%, and for the second generation of beetles – 11.6%.

Differences in the reduction intensity of the Colorado beetles  
on the two potato fields

Tab. IV

Developmental stage	Per cent of reduced individuals	
	eastern field	western field
Eggs	13.8	8.5
$L_1$	53.2	53.9
$L_2$	1.3	12.0
$L_3$	4.8	9.0
$L_4$	4.2	2.5
Total	77.3	85.9

Differences in the reduction intensity are also quite evident (Tab. IV). The eastern field had its reduction about 8% smaller than the western field. In the period of the egg development the elimination was more intensive in the eastern field. The  $L_1$  was in both the fields reduced with a similar intensity. In further development stages the difference was clearly marked in both the fields. The elimination intensity of  $L_2$  in the western field was nearly 10-times higher than in the eastern one, and in the case of  $L_3$  almost twice as high. Differences in the reduction of individual stages in both the investigated fields support the supposition that there were three sets of factors reducing the Colorado beetle. A somewhat weaker reducing activity of the insects using the Colorado beetle eggs as an alimentary basis was compensated in the western field by a stronger reduction in the next stages of the larval development. The existence and activity of such reducing groups had a particular significance because larvae of the first stage do not destroy the potato leaves. This problem requires further, detailed investigations.

The above analysed differences in the course of the Colorado beetle reduction were more or less the same in all the separate periods (Fig. 7, 8). The



course of reduction in the eastern field was mainly characterized by an increasing per cent of individuals reduced in the first two development stages (the eggs and  $L_1$ ). The further course of reduction affected the final result in a lesser degree (Fig. 7). In the western field (Fig. 8) the continuation of the intensive reduction is quite striking till the moment when the third larval stage was reached. The final result of the reduction represented here the result of the elimination taking place from the moment when the eggs were laid to the end of the third larval stage.

### THE BACKGROUND OF THE REDUCTION PROCESSES

The investigations and analysis of the data concerning the Colorado beetle reduction were carried out in various aspects. Van den Bruel and Moens (1959) established the difference in the reduction intensity of the Colorado beetle between two regions characterized by different soil and microclimate. The differences in the reduction intensity between two adjoining fields recorded in our investigations were similar to the ones quoted by Van den Bruel and Moens (1959) for different types of soil. However in our case on both investigated fields environmental factors were the same. Only the possibility of a search for biocenotic and populational factors may be taken into consideration.

The elaboration of biocenotic problems connected with the Colorado beetle reduction (Kaczmarek 1955, Franz 1957, Węgorzek 1959) was based on quantitative data concerning the reduction of the Colorado beetle and descriptive, general information on the state of the biocenose and this contributed to the fact that the conclusiveness of statements, biocenotic in character, put forward in the above mentioned papers could not be treated as complete. Because the elaboration of the quantitative materials concerning the biocenose of the potato field has not been finished yet we supply here only results concerning the populational aspects of the Colorado beetle reduction.

The egg reduction (Fig. 9). presents in our investigations a phenomenon depending on the density similarly to what was proved by Kaczmarek (1955). The reduction had a character approximately invertly proportional to the density of eggs although it was somewhat higher for the highest densities. However our results differ significantly from the ones obtained in experimental conditions. A striking difference occurred first of all in low densities of eggs where the reduction observed in natural conditions was three times lower than it was recorded in experimental conditions. These differences disappeared only when we considered the highest densities amounting to 100 or more eggs per one plant.

A simple character of the observed dependence did not contribute to the



facilitation of an ecologic interpretation of the phenomenon. For both in Kaczmarek's experiments (1955) and in our investigations the number of destroyed eggs did not change proportionately to changes in the density — it was more or less constant. The regularity, recorded by the application of the method of percentage, had to a certain degree an apparent character. For the density of eggs did not determine their attractiveness for the predators as a similar number of eggs was destroyed in large and small layers. In such a situation the research for density-dependent reactions held out little hope and the problem of reasons for the egg reduction of the Colorado beetle requires further investigations.

The effect of the density of larvae on their reduction. The intensity of the reduction of  $L_1$  as compared with the reduction of older was very high.  $L_2-L_4$  showed considerable similarities in the course of the seasonal reduction and consequently they were treated together in the following analysis.

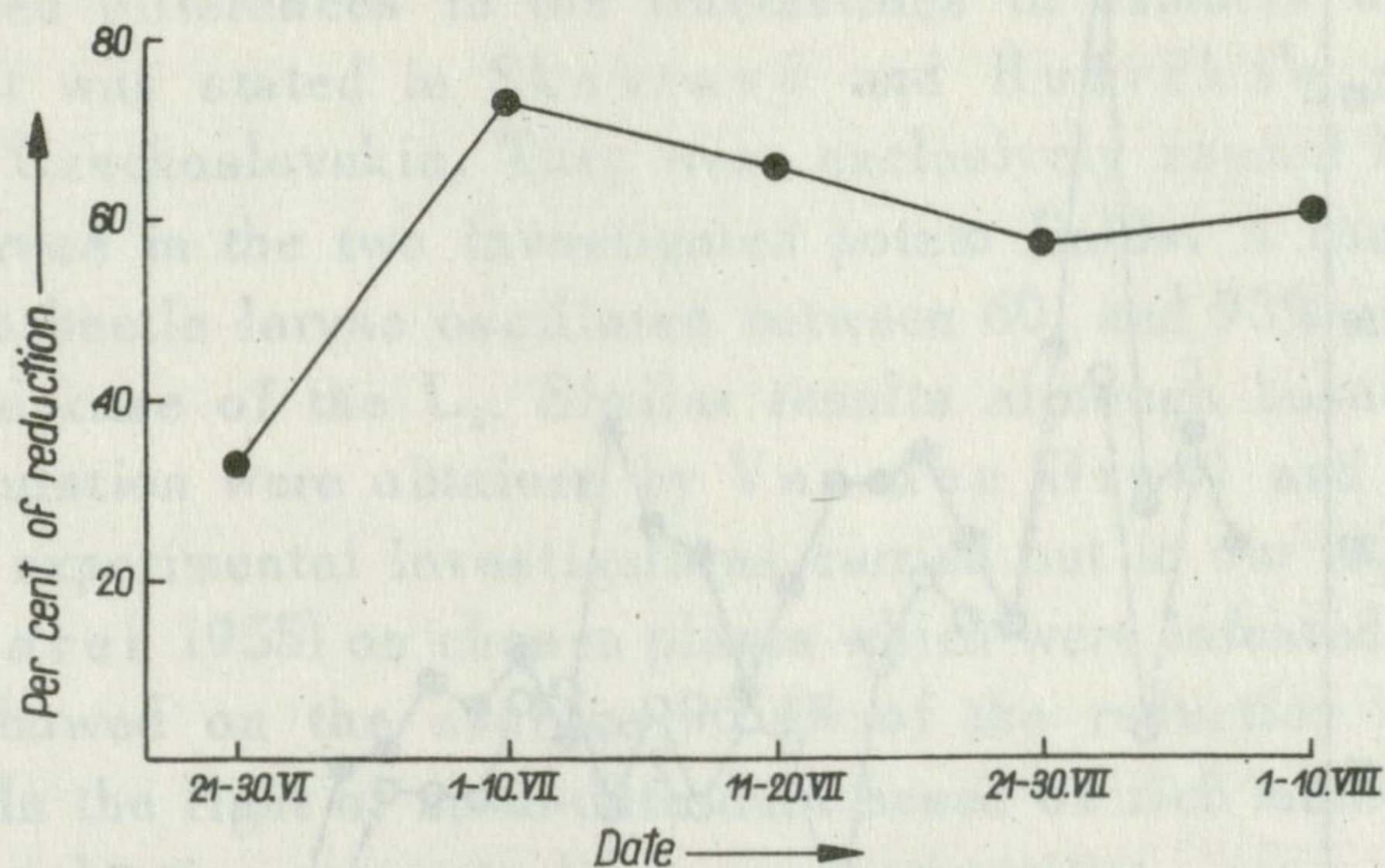


Fig. 10. Seasonal changes in the first instar larvae reduction of the Colorado beetle

The reduction of  $L_1$  in June, immediately after this stage had appeared, was still low (Fig. 10), however in the course of ten days it increased to more than 70% when this larval stage reached its numerical peak. In the course of a month the reduction per cent of  $L_1$  dropped down to 60%. This drop was accompanied by a decrease in the number of  $L_1$  which is however much more considerable than the recorded drop in the reduction of these larvae. And so the reduction intensity did not decrease but on the contrary it increased.

Older larvae ( $L_2-L_4$ ) showed a connection between the reduction intensity and density. However when in the case of the egg reduction the number of reduced eggs oscillated in the range of the four-fold value of the minimal reduction and usually the changes were to about 1.5% of the minimal value, then in the case of the reduction of older larvae the highest number of eliminated



larvae was twenty times higher than the minimal reduction. At the same time we recorded an increase in the per cent of reduced larvae together with their density. Larvae of the Colorado beetle and particularly  $L_3$  and  $L_4$  dominated, among the epiphytic macroentomofauna. Owing to this the zoophages quickly reacted positively on an increase in numbers of the Colorado beetle larvae and used them more and more intensively as an alimentary basis.

The second factor increasing simultaneously the accessibility of the Colorado beetle larvae for zoophages is the change in the space structure of the population during the season. Populations of the Colorado beetle are characterized by a significant degree of aggregation, spots and focuses with a high density degree are quite striking in the field. This feature, expressed quantitatively (Fig. 11), clearly changed in the course of the season. The

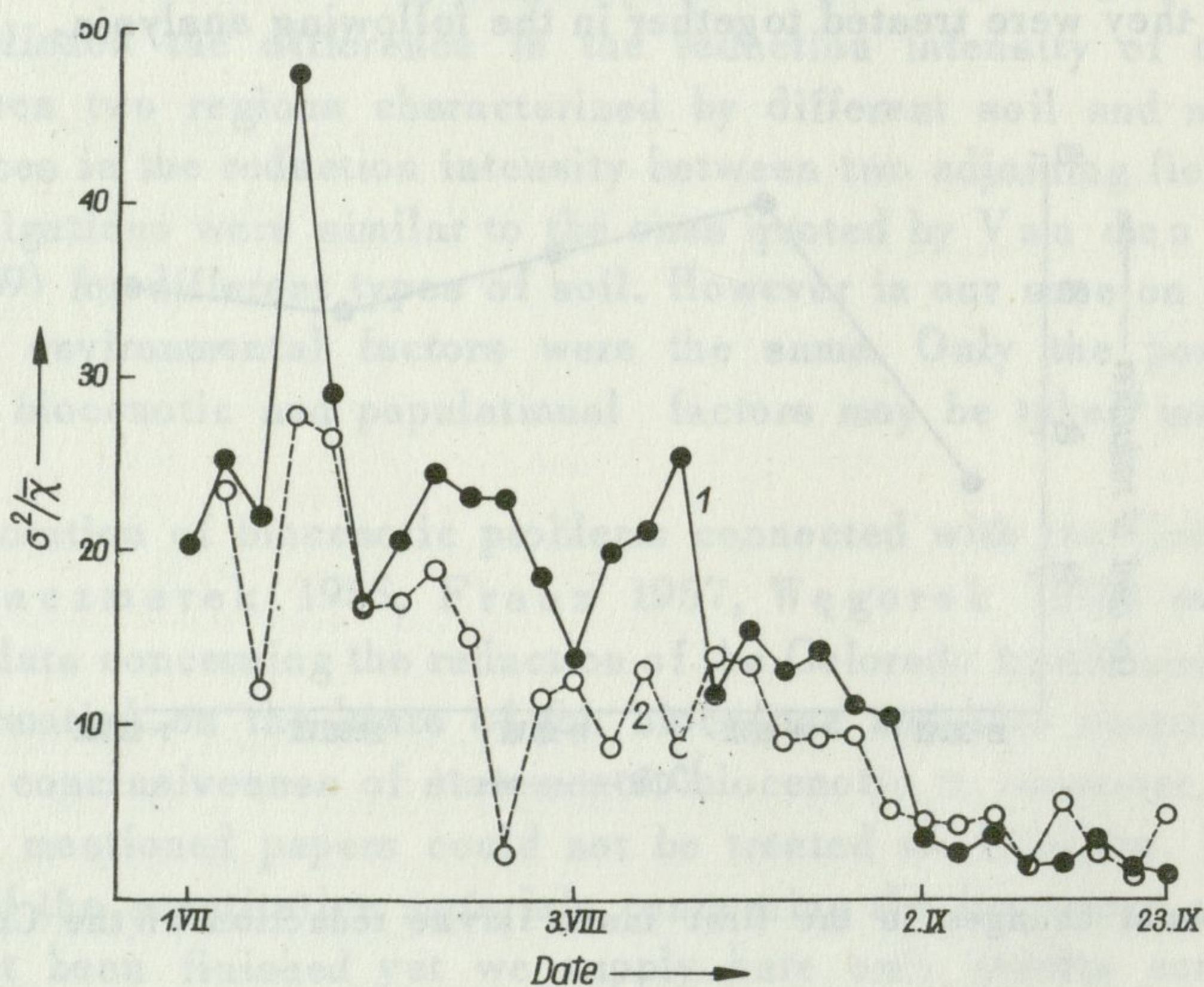


Fig. 11. Seasonal changes in the aggregation of the Colorado beetle larvae  
1 - eastern field, 2 - western field

highest degree of aggregation was recorded in the first half of July, and in August there followed a regular decrease in the ratio  $\frac{\sigma^2}{\bar{x}}$  and that indicated a gradual dispersion of the Colorado beetle aggregations. In September the distribution of the Colorado beetle was nearly random.

The change of the distribution from aggregational for a nearly random one with a simultaneous, considerable increase in the density of the Colorado beetle larvae caused that the contacts of the Colorado beetle with predators



were intensified in the course of time and this was followed by an increased reduction of the Colorado beetle larvae.

#### DISCUSSION OF RESULTS

The fenology of the course of the Colorado beetle appearance in the two investigated potato fields had a similar character. The initial invasion of hibernating beetles and the number of eggs laid by them were in the two fields nearly identical. The appearance of larvae commenced 10–15 days later than in France (Arnoux and Le Berre 1963) and at the same time as in the vicinity of Prague in 1965 (Skuhřavý and Makeš 1965). The development period of the larvae lasted 100 days and so considerably longer than in Czechoslovakia (60 days) and more than twice as long as in France. Only one generation managed to develop from the eggs laid from June to 10th August. Larvae developed from eggs laid later did not finish their development. Beetles from the summer generation did not lay any eggs.

The recorded differences in the fluctuations in numbers were not so considerable as it was stated in Skuhřavý and Ružička's paper (1965) for two regions in Czechoslovakia. They were exclusively caused by the reduction intensity of larvae in the two investigated potato fields. A complete reduction of the Colorado beetle larvae oscillated between 60, and 93% and the strongest one was in the case of the  $L_1$ . Similar results although based on a different method of calculation were obtained by Van den Bruel and Moens (1959). The results of experimental investigations carried out in our region in previous years (Kaczmarek 1955) on chosen plants which were infested by the Colorado beetle eggs showed on the average 96.4% of the reduction of the Colorado beetle larvae. In the light of up-to-date data based on rich material such a high per cent of the reduction seems to be an overestimation.

The reasons for the egg reduction in spite of distinct regularities in its course seem to be now unclear, on the other hand as far as larvae, particularly older ones, are concerned there can be clearly seen a visible effect on the size of the reduction both of the increasing number and of a change in the spatial structure of the population from aggregational for a random one. An increased number and accessibility of the Colorado beetle larvae contribute to their greater attractiveness to the predators.

#### CONCLUSIONS

1. The newly worked out method of estimate of the natural reduction of the Colorado beetle enables to analyse various aspects of the reduction processes.
2. The natural reduction of the Colorado beetle in the investigated fields reached up to 93% of the initial figure of eggs and underwent regular changes in the course of the season.



3. The survival of Colorado beetle larvae in early summer is greater than in the end of the vegetative season; the reduction increases in course of time.
4. The reduction of the Colorado beetle larvae was intensified simultaneously with an increase in their density and gradually more random distribution.
5. In 1965 the development period of the Colorado beetle included 100 days during which developed only one generation.
6. The fertility of females estimated in natural conditions amounted to about 707 eggs per one female.

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#### DYNAMIKA LICZEBNOŚCI I REDUKCJA STONKI ZIEMNIACZANEJ (*LEPTINOTARSA DECEMLINEATA* SAY) W WARUNKACH NATURALNYCH

##### Streszczenie

W 1965 r. w Zakładzie Agreologii w Turwi prowadzono badania nad dynamiką liczebności i redukcją stonki ziemniaczanej w warunkach naturalnych. Badaniami objęto dwa jednohektarowe pola położone po dwóch stronach pasa zadrzewień śródpolnych



przebiegającego w kierunku N-S. Badane pola nie były objęte zwalczaniem chemicznym. Informacje dotyczące dynamiki liczebności stonki ziemniaczanej zbierano w trzydniowych odstępach, postępując według ustalonego schematu, gwarantującego równomierne pokrycie całego pola siatką prób. Oceniano liczebność jaj, wszystkich stadiów larwalnych i imagines obu pokoleń z podziałem na samce i samice.

Ocenę redukcji przeprowadzono w oparciu o dane dotyczące dynamiki liczebności. Aby dane te można było porównywać w przypadku jaj i larw, podzielono je przez czas trwania poszczególnych faz rozwojowych. Przebieg dynamiki liczebności chrząszczy pokolenia zimującego jest podobny na obu polach i dzieli się na dwa okresy: pierwszy o stałym poziomie liczebności, drugi charakteryzujący się wzrostem, a następnie spadkiem liczebności (fig. 1). Chrząszcze pokolenia letniego pojawiają się na początku sierpnia, a ich liczebność w krótkim czasie osiąga maksimum. Szczyt liczebności jaj przypada na ostatnią dekadę czerwca (30,67 jaj/m<sup>2</sup> fig. 2). W jednym złożu występuje 30–40 jaj. Całkowita ilość jaj wynosi 304,08 jaj/m<sup>2</sup> i 76,02 jaj na jedną roślinę ziemniaka. Jedna samica składa 707,2 jaj, co w porównaniu ze znacznie wyższymi danymi laboratoryjnymi (Węgorek 1959, 1965), wskazuje na ograniczenie w warunkach naturalnych potencjalnych możliwości rozrodczych stonki ziemniaczanej. Pierwsze larwy (L<sub>1</sub>) stwierdzono 28 VI, w 9 dni po zaobserwowaniu pierwszych złożeń jajowych. Przebieg dynamiki liczebności poszczególnych stadiów larwalnych charakteryzuje się przesunięciami w czasie w stosunku do stadium wcześniejszego. Różnice w liczebności między polem wschodnim i zachodnim są wyraźne w przypadku stadium L<sub>1</sub> i L<sub>2</sub>, natomiast dynamika liczebności stadium L<sub>3</sub> i L<sub>4</sub> kształtuje się podobnie na obu polach (fig. 3–6).

Krzywa redukcji we wszystkich przypadkach charakteryzuje się podobnym przebiegiem, w kształcie litery L, co wynika z niejednakowego nasilenia redukcji poszczególnych stadiów rozwojowych.

Najsilniej redukowane jest w przypadku larw stadium L<sub>1</sub> (przeciętnie 53,6% zniesionych jaj). Dla starszych stadiów rozwojowych (L<sub>2</sub>, L<sub>3</sub>, L<sub>4</sub>) natężenie redukcji stopniowo spada (do 3,33% dla L<sub>4</sub>). Stosunkowo niewielka jest redukcja jaj (przeciętnie 11,2%). Nasilenie redukcji wzrasta w ciągu sezonu. Redukcja na obu polach przebiegała niejednakowo. Ogólnie redukcja na polu wschodnim była o ponad 8% mniejsza niż na zachodnim. Różnice te wynikają głównie z odmienności czynników biocenotycznych badanych pól. Redukcja larw wzrasta wraz ze wzrostem zagęszczenia. W ciągu sezonu struktura przestrzenna populacji ulega zmianie ze skupiskowej na rozproszoną (fig. 4). Stwierdzono zależność między wzrostem redukcji a wzrostem dyspersji populacji stonki.

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