

The effects of feeding damage in ragweed *Ambrosia artemisiifolia* (Asteraceae) on populations of *Zygogramma suturalis* (Coleoptera, Chrysomelidae)

S.Ya. Reznik

Zoological Institute, Academy of Sciences, Leningrad 199034 USSR

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Summary. Field sampling indicated that the number of eggs laid by a *Zygogramma suturalis* female within a sampling plot correlated inversely with the mean degree of ragweed damage. Feeding on extensively damaged ragweed in the laboratory caused a drop in oviposition intensity, and a considerable proportion of females completely stopped oviposition. Feeding on slightly damaged ragweed had no significant effect on oviposition intensity. Ovipositing females preferred to feed on the intact ragweed and lay their eggs close to it. The locomotory activity of ovipositing females was significantly higher on highly damaged ragweed whereas non-ovipositing (diapausing) females and males were behaviourally indifferent to the extent of ragweed damage. Under natural conditions, ovipositing females more frequently left damaged host plants for less damaged ones. If the degree of ragweed damage is high over a large area, the insects that were unable to find undamaged plants for several days oviposited less and some females entered diapause. The adaptive effect of these reactions is a decrease of population density in advance, before it might drop as a result of starvation. These results are in agreement with the second model of insect reaction to the damage-induced changes in a host plant (Edwards and Wratten 1987).

Key words: Induced defence – Behaviour – Diapause – *Zygogramma* – *Ambrosia*

Studies of insect reactions to changes induced in their host plants by feeding have lately received much attention in entomological investigations (see reviews by Edwards and Wratten 1983, 1985, 1987). Folivorous insects and mites as a rule prefer to feed on undamaged plants (Dicke 1986; Harrison and Karban 1986; Raupp and Sadof 1988, 1989; Croxford et al. 1989). The rate of larval development, weight of pupae and female fecundity are decreased as a result of feeding on previously damaged plants (Haukioja and Niemela 1977; Haukioja 1980; Raupp and Denno 1984; Raupp and Sadof 1988;

Gibberd et al. 1988; El-Bassiouny 1989). Frequently both ethological (preference) and the physiological (suitability) reactions are manifested (Parker 1984; Bergelson et al. 1986; Prins et al. 1987). Contrasting cases have, however, also been reported, where the absence of a wound-induced defense (Chapin et al. 1985), and preference for damaged plants are observed (Carroll and Hoffman 1980). Egg-laying females may discriminate between damaged and intact host plants, laying eggs mostly on the latter (Ives 1978; Taylor and Forno 1987; Forno and Bourne 1988), although exceptions may occur (Kumar 1986).

Despite the considerable number of papers on this topic, there is a lack of empirical data, and especially of studies in which different forms of reactions to natural and artificial damage of host plant are studied both in the field and under laboratory conditions. The reaction to host plant damage could have important consequences for the population dynamics of the herbivore (Wratten et al. 1988; Edelstein-Keshet and Rausher 1989) and is particularly important in the biological control of weeds (Crawley 1989).

Zygogramma suturalis F. (Coleoptera, Chrysomelidae) was introduced into the USSR from the U.S.A. for biological control of ragweed, *Ambrosia artemisiifolia* D.C. (Kovalev and Medvedev 1983). The herbivore successfully acclimated and was able to suppress and even exterminate the weed when *Z. suturalis* population density was sufficiently high (Kovalev 1989). Recently, ecological field and laboratory studies found different types of reactions in this herbivore to ragweed damage (Reznik 1985, 1989). This paper is the first to summarize the results of all studies on the reaction of *Z. suturalis* to damaged host plants and includes both original and previously published data and interpretations.

This investigation attempts to answer five questions:

1. Do wound-induced changes in leaf quality affect the feeding preferences, ovipositional selectivity and, consequently, population dynamics of *Z. suturalis* in natural conditions?
2. Do wound-induced changes affect the fecundity

and, possibly, diapause of females under laboratory conditions?

3. Do wound-induced changes affect the feeding behavior and preferences of *Z. suturalis* under laboratory conditions?

4. Do the reactions of males, ovipositing females and diapausing females to wound-induced changes differ in any way?

5. Do the results of this investigation agree with earlier models of insect reactions to damage-induced changes in a host plant (Edwards and Wratten 1987)?

Materials and methods

Field studies were conducted in 1983–1984 in the vicinity of the first introduction site of *Z. suturalis* (USSR, Stavropol region). Most of the cultivated fields and uncultivated sites were overgrown with ragweed (mean phytomass about 300 g/m²). Insect and host material for laboratory studies were collected in the same area. Ragweed was intact or damaged either naturally by adults and/or larvae of *Z. suturalis* or artificially by manually cutting a part of the leaf blade from each leaf. The degree of ragweed damage was evaluated visually by estimating the relation of the area eaten to primary leaf area. Four grades of ragweed damage were evaluated: intact (zero or less than 1% visible damage), slight damage (1–5%), medium damage (6–50%) and highly damaged (more than 50%).

In every sampling of 10–200 plots of 0.1 m² the number of eggs, larvae and adults of *Z. suturalis*, ragweed phytomass, percentage of ragweed damage and some other parameters were estimated. Sampling of plots was either regular or random.

The laboratory experiments were carried out in 1985–1987 at room temperature (20–26°C) and natural daylight. To evaluate fecundity, females were placed individually in Petri dishes, each containing ragweed leaves collected from plants with different degrees of damage. To prevent dehydration, the leaf petioles were wrapped in wet cotton and polyethylene. Laid eggs were counted and host material was renewed every second day.

To describe behavioural characteristics, performance was registered periodically (every 10–15 min) throughout the daylight period (from 8 a.m. to 9 p.m.). *Z. suturalis* ovipositing females, diapausing females or males were placed individually in Petri dishes or in choice cages which consisted of two sections 10 × 10 × 2.5 cm connected by a 15-cm pathway. Intact ragweed leaves were put into one section, while the other contained the leaves of a damaged plant. The position of an individual beetle in one of the two sections and the behaviour of a beetle (feeding, motion, rest) were recorded. The number of eggs laid was estimated for each section.

Not less than 10–15 insects were simultaneously monitored for 6–8 days or more in every replicate of each experiment. Results were averaged. Due to somewhat unstable photothermal conditions the experimental and control series were always run simultaneously. The photothermal conditions in different Petri dishes and cages were nearly identical.

Statistical analysis included Pearson's correlation analysis, Student's *t*-test (for quantitative characteristics) and the χ^2 test (for qualitative ones).

Results

Field sampling

In the field the number of eggs laid by a *Z. suturalis* female within a sampling plot was inversely correlated with the mean rate of ragweed damage. As an example, Fig. 1 demonstrates the results of a typical sample. Cor-

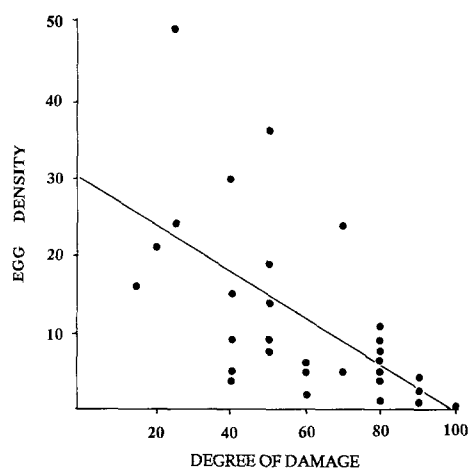


Fig. 1. The effect of ragweed damage upon the number of *Z. suturalis* eggs within a plot (sample 13.07.1983). Each point represents one plot. Also shown is the regression line ($Y = 29 - 0.3X$, $r = -0.59$, $P < 0.001$)

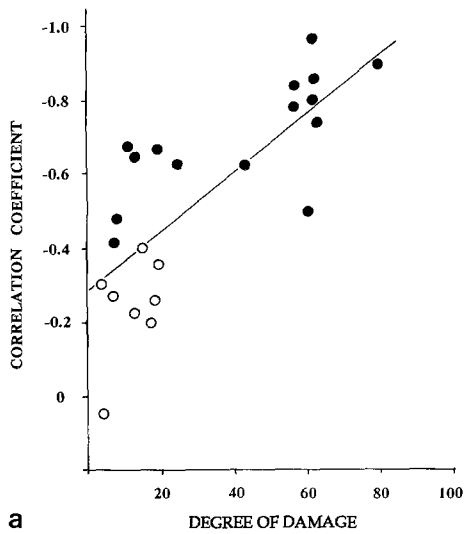
relation between the degree of damage and the number of eggs is inverse in all samples although the correlation coefficient depends on the year and the field studied (mean $r = -0.30$ to -0.50), but the absolute value of r and its significance depend on the mean degree of ragweed damage within the field studied (Fig. 2a).

Ragweed damage was accompanied by a decrease in phytomass (mean $r = -0.40$ to -0.60), the latter, in turn, affecting the number of eggs laid (mean $r = 0.55$ to 0.60). It therefore seemed necessary to calculate the partial correlation coefficients that characterise the direct correlation between degree of damage and number of eggs (independent of ragweed phytomass). The partial correlation coefficients were found to depend on the mean degree of ragweed damage and are significant only for fields with a mean degree of damage no less than 60% (Fig. 2b).

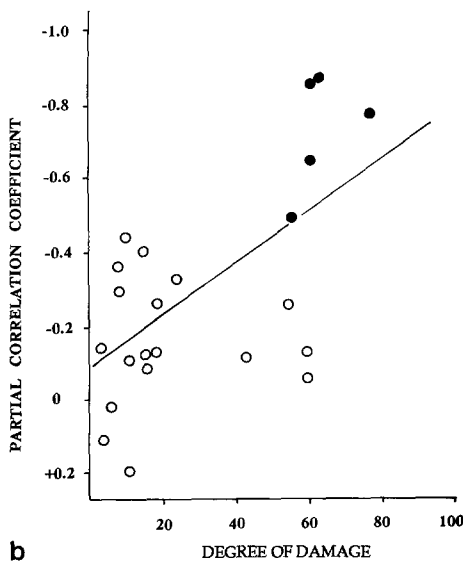
The oviposition intensity (the relation of the number of eggs to the number of beetles within the plot) depends upon the degree of ragweed damage. Table 1 presents mean values of oviposition intensity, calculated for the plots with small, medium and large amounts of damage in several samples within the same field.

Laboratory experiments

Z. suturalis females forced to consume highly damaged ragweed also suffered major reductions in oviposition intensity in the laboratory. Experiments carried out at different times with different samples of *Z. suturalis* revealed that the number of eggs laid daily decreased after feeding on damaged ragweed (Fig. 3). A considerable proportion of females completely stopped oviposition (Fig. 4). This effect is reversible: upon transfer of a number of females from feeding on damaged ragweed to undamaged plants a return to the control level was observed in both the mean fecundity (faster) and the percentage of ovipositing females (slower) (Figs. 3, 4). If a choice between both damaged and intact ragweed were



a



b

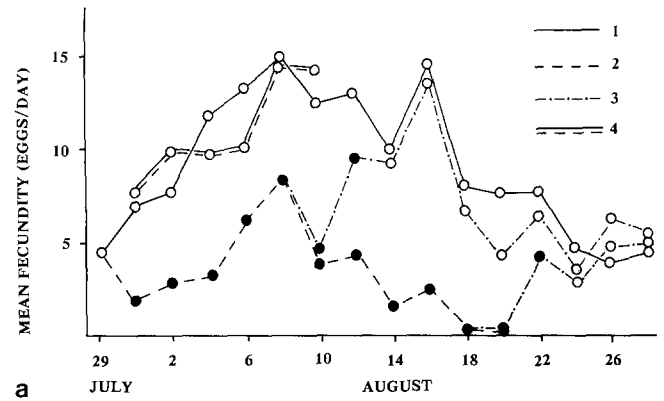
Fig. 2a, b. The effect of mean degree of ragweed damage within the field upon the value of Pearson's correlation coefficient r between damage and egg density (sampling 1983–1984). Each *symbol* represents one sample. *Full circles* indicate that r is significant ($P < 0.05$). The regression lines are also shown. **a** Correlation coefficients ($Y = -0.3 - 0.008 X$, $r = -0.75$, $P < 0.001$). **b** Partial correlation coefficients excluding the effect of ragweed phytomass ($Y = -0.08 - 0.007 X$, $r = -0.61$, $P < 0.01$)

Table 1. Mean oviposition intensity (eggs/beetles) of *Z. suturalis* females on sampling plots with different rates of ragweed damage

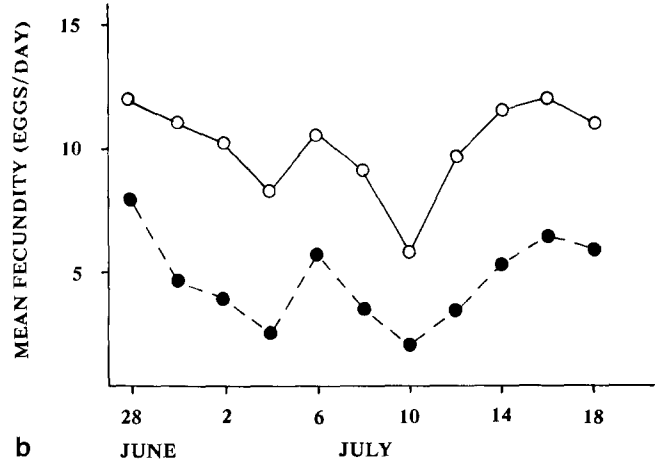
Date	Number of plots ¹			Oviposition intensity ²		
	SL	ME	HI	SL	ME	HI
17.07	10	15	14	7.2 ^a	0.8 ^b	0.01 ^c
25.07	6	15	8	6.7 ^a	1.1 ^b	0.02 ^c
31.07	10	13	8	11.0 ^a	3.2 ^b	0.34 ^c
13.08	10	12	7	16.4 ^a	6.1 ^b	0.64 ^c
20.08	10	12	8	13.4 ^a	2.9 ^b	0.12 ^c

¹ SL – slight damage (1–5%), ME – medium damage (6–50%), HI – highly damaged (more than 50%).

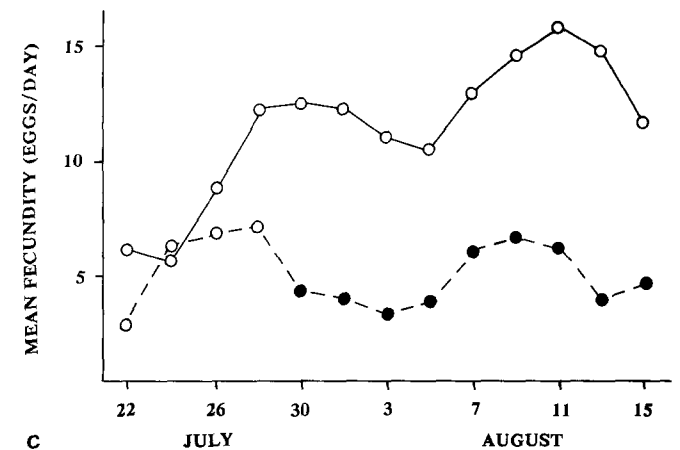
² Values followed by different superscript letters in the same row are significantly different at the $p = 0.01$ level by Student's t -test



a



b



c

Fig. 3a–c. The effect on the fecundity (eggs/day) of ovipositing *Z. suturalis* females of highly damaged ragweed offered as food. Females were: 1, on undamaged ragweed (control); 2, on highly damaged ragweed; 3, transferred from damaged to undamaged ragweed; 4, offered a choice between damaged and undamaged ragweed. The separate graphs show observations on **a** mature females; **b** females after emergence from hibernation; **c** young females not yet mature at the beginning of the experiment (see text for further details). *Full circles* – the experimental group differ significantly from controls ($P < 0.05$), Student's t -test

offered, the mean fecundity was not significantly different from that in the control (Fig. 3).

In choice cages, ovipositing *Z. suturalis* preferred to remain in the section with intact ragweed, and to feed and lay their eggs close to it (Table 2). The locomotory activity of ovipositing females was significantly higher in

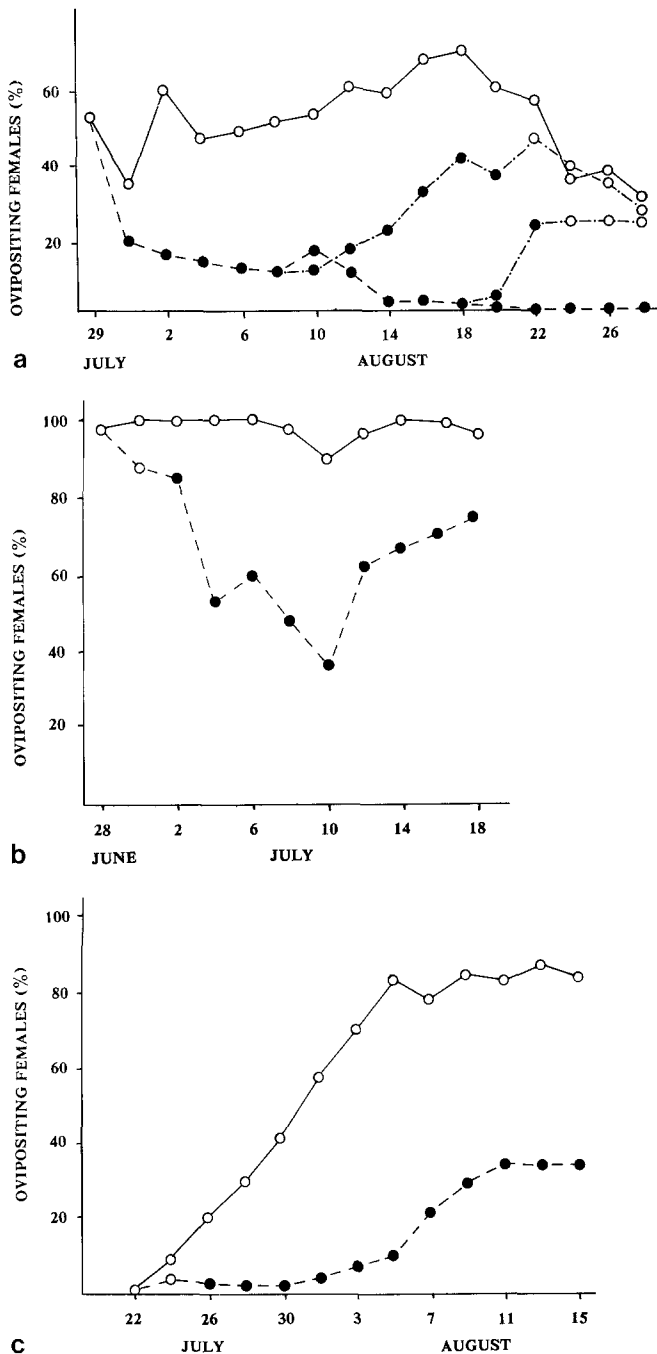


Fig. 4a-c. The effect of feeding on highly damaged ragweed on the percentage of ovipositing *Z. suturalis* females. Results presented as in Fig. 3

the sections with highly damaged ragweed. Non-ovipositing (diapausing) females were indifferent to the ragweed damage. Dissimilarities in the behaviour of the females in sections U and D of series 2 may be explained by the presence of a number of maturing females among the non-ovipositing ones.

In series 1 and 2, the ragweed was naturally damaged by beetles and larvae up to 70%. In series 3, the ragweed was artificially damaged by cutting off about half of each leaf, 6 days before the experiment. Such a high degree of damage was required to elicit reactions similar to those

of females toward naturally damaged leaves (Fig. 2). *Z. suturalis* ovipositing females reacted both to natural and artificial damage of the host plant (Table 2). The somewhat less pronounced differences in series 3 are possibly due to a reduced degree of damage. According to the results of series 4, females did not differentiate between intact ragweed and ragweed with up to 5% artificial damage.

Reaction to host plant damage was not only revealed in choice cages. Ten ovipositing females placed individually for a month in Petri dishes containing two sets of ragweed leaves (intact and 70% damaged) preferred to feed, rest and move on the intact plant rather than on the damaged ragweed (75% of whole time spent on ragweed, $P < 0.001$). Meanwhile diapausing females and males were practically indifferent in their choice (50% and 47%, $P > 0.05$).

When ovipositing females were deprived of choice by offering only damaged or only intact ragweed, the effect of host plant quality upon the locomotory activity was evident (Table 3). Females which fed on damaged ragweed moved about twice as much. The difference between the sets of observations can be explained by temperature, which was the same in the experimental and in control groups for each observation (see Material and methods).

Discussion

Ovipositional preference for less damaged host plants has been observed in some other insects (Ives 1978; Taylor and Forno 1987; Forno and Bourne 1988). An increase in population density is not enough by itself to cause a decrease in oviposition intensity of *Z. suturalis* females when feeding on intact ragweed (Reznik 1985). This means that the reactions observed in the present study were most likely the result of host plant damage, not insect pheromones.

A pronounced dependence of mean oviposition intensity on the degree of damage (Table 1) indicates that the greater proportion of eggs laid on undamaged ragweed was not caused by a dislocation of the entire population of *Z. suturalis*, but was the result of a sharp decrease in the mean oviposition intensity under unfavorable conditions i.e. a drop in fecundity or migration of ovipositing females. Data obtained from dissection of females collected in plots with different degrees of ragweed damage showed that the lower the degree of damage, the higher the percentage of ovipositing females (Vinogradova and Bogdanova 1989). This effect could be a result of two different processes i.e. migration of ovipositing females to the intact host plants and/or decrease of oviposition on plants with damage.

Feeding on highly damaged ragweed in the laboratory caused a drop in oviposition intensity (Figs. 3, 4). The differences between the three sets of observations, (*a*, *b* and *c*) can be related to differences in the makeup of samples: in *a* females of the first generation were used and the dynamics of the percentage of ovipositing females in the control group reflects the beginning of

Table 2. The effect of damaged ragweed on the behavior of *Z. suturalis* (preference tests)

Series	Physiol. state of females ¹	Percentage time spent in sections with damaged and undamaged ragweed		Percentage time spent in:				Percentage eggs laid in sections with damaged and undamaged ragweed	
		U ²	D	feeding		locomotion		U	D
				U	D	U	D		
1	Ov	83a ³	17b	3.0 ^a	0.3 ^b	11 ^a	44 ^b	82 ^a	18 ^b
1	Di + Mt	64a	36b	0.8 ^a	0.2 ^a	1 ^a	18 ^b	—	—
2	Ov	82a	18b	— ⁴	—	—	—	69 ^a	31 ^b
2	Di	52a	48a	—	—	—	—	—	—
3	Ov	72a	28b	—	—	—	—	65 ^a	35 ^b
3	Di	48a	52a	—	—	—	—	—	—
4	Ov	53a	47a	2.8 ^a	3.1 ^a	6 ^a	5 ^a	52 ^a	48 ^a

¹ Ov – ovipositing, Di + Mt – diapausing and maturing, Di – diapausing

² U – section with undamaged ragweed, D – with damaged ragweed

³ Values followed by different superscript letters in the same row in the next "U" and "D" columns are different at the $p = 0.05$ level (χ^2)

⁴ No data

Table 3. Host plant damage influence on the locomotory activity of *Z. suturalis* ovipositing females (no choice)

Replicate	Percentage of time spent on movement on the ragweed ¹	
	Damaged	Undamaged
1	6.6 ^a	11.4 ^b
2	2.8 ^a	5.3 ^b
3	14.2 ^a	27.8 ^b
4	12.7 ^a	20.5 ^b

¹ Values followed by different superscript letters in the same row are different at the $p = 0.05$ (χ^2)

diapause, which is normally observed in mid-August (Reznik 1985; Vinogradova and Bogdanova 1989); in *b* females after hibernation were used, all of them beginning oviposition at the start of the experiment; in *c* young beetles of the next year first generation, which were not yet mature and the beginning of the experiment, were used. Relative decreases in percentage of ovipositing females (as referred to the control) and the decrease in the number of eggs laid daily are apparent in all three sets of observations. Feeding on previously damaged or stressed host plants causes a decrease in fecundity in various herbivores including Chrysomelidae (de Wilde et al. 1969; Jones and Coleman 1988; Raupp and Sadof 1988; El-Bassiouny 1989).

The inhibition of oviposition observed is not a simple interruption of the maturation of ova. According to dissections conducted by E.B. Vinogradova (unpublished), a hypertrophied fat body indicates the occurrence of true diapause. Generally an unfavorable environment provokes diapause (Danilevski 1965; Tauber et al. 1986; Zaslavski 1988). De Wilde et al. (1969) demonstrated that the induction of diapause is more pronounced in *Leptinotarsa decemlineata* Say after feeding on old potato leaves. Possibly, feeding damage in ragweed provokes aestivation i.e. brief summer diapause, which is quite often observed in *Z. suturalis* (Vinogradova and Bogdanova 1989). In some insects diapause may manifest

itself in minor reversible delays of development or oviposition. For example, in *Dendrolimus pini* L. diapause may last from a few days to 2 months (Danilevski 1965); in *Oedipoda miniata* Pall. a continuous series of transitions from extensive activity, through intermediate states, to pronounced diapause was observed (Pener and Orshan 1980).

Reversibility of the decrease in oviposition intensity and a lack of difference between controls and the insects given a choice between damaged or intact ragweed (the latter is preferred as apparent from Table 2) allow us to conclude that serious damage of ragweed over large areas is needed to provoke oviposition inhibition i.e. the females must have no chance of finding an intact or slightly damaged host plant for several days.

The preference for undamaged plants in feeding and oviposition observed in *Z. suturalis* is a feature observed in many insects and mites (Ives 1978; Parker 1984; Bergelson et al. 1986; Dicke 1986; Harrison and Karban 1986; Prins et al. 1987; Taylor and Forno 1987; Forno and Bourne 1988; Croxford et al. 1989). It is noteworthy that avoidance of highly damaged plants is seen only in ovipositing *Z. suturalis* females, while the diapausing females and males are indifferent in their food choice between damaged and intact ragweed. Given the strong effect of food quality and reduced feeding intensity on beetle fecundity and low starvation tolerance of larvae, the ability of ovipositing females to avoid damaged plants seems highly adaptive.

The process by which ovipositing females concentrate on undamaged plants can be explained by orthokinesis: i.e. changes in the speed or frequency of locomotion depending on the environment (see review: Visser 1988). In the present study, locomotory activity increased upon feeding on damaged host plant (Tables 2, 3). Wound-induced changes in plants may increase movement in herbivores (Edwards and Wratten 1983; Schultz 1983). Bergelson and Lawton (1988) and Raupp and Sadof (1989), however, found no difference in activity patterns of herbivores on control and damaged branches.

Slightly damaged ragweed caused no oviposition inhibition and was not avoided by the ovipositing females.

The quality of ragweed seems to decrease only after a large amount of damage. So far it is unclear what processes underlie this reaction: an increase of the concentration of antifeedants, of toxins, of enzyme inhibitors, or a drop in the nutrient content. The absence of reaction in slightly damaged ragweed speaks in favour of the last suggestion.

Summarizing the results of field sampling and laboratory experiments, the ethological and physiological response of *Z. suturalis* to damaged plants under natural conditions can be accurately described. Locomotor activity of ovipositing females increases, and the females more frequently leave host plants when on damaged plants. If the degree of ragweed damage is high over a large area, the insects that are unable to find undamaged plants for several days decrease oviposition intensity and some females enter diapause. If such females find a slightly damaged host plant, however, they do not leave it and oviposition intensity gradually returns to the former level. The adaptive essence of these reactions, obviously, is the decrease of the herbivore population density in advance, before it might drop as a result of starvation.

In cases of overpopulation (more than 500–1000 beetles per kg ragweed) a “population wave” occurs, which moves at a speed up to 3 m/day and leaves behind an area of complete extermination of ragweed (Kovalev 1988). However, this is an extremely rare event in agrocenoses because of insecticide treatment and crop rotation (Reznik 1989). Overpopulation is possible despite the regulatory mechanisms described above, since they function with a delay i.e. the females respond to surplus density only when larvae have reached the third instar and have already caused noticeable damage to the ragweed, that will, however, increase further. In the native area under the control of specific predators and parasites overpopulation is perhaps never achieved despite the delayed response. In new conditions (excess of food and absence of specific eliminative factors), regulation based on oviposition intensity and selectivity is not likely to control population density.

The existence of overpopulation is possible, according to our results, only during a short period from the emergence of young adults of the first generation to the beginning of their oviposition. During this period the majority of females display little or no reaction to the degree of damage, and the effects of current oviposition have not yet taken full effect. Only in these circumstances can ragweed be fully exterminated by adults under natural conditions. Observations confirm this prediction – the wave “dissipates” in early August (Kovalev 1988).

In conclusion, the results presented here are in agreement with the second model of insect reaction to the damage-induced changes in a host plant (Edwards and Wratten 1987). Field sampling revealed a graded reaction to the degree of damage. The redistribution of the population density of the insect occurs as a result, causing the dispersed damage of host plants. Two reactions can be inferred from the observed effects of host plant damage on the insects. The first is an ethological reaction, as in the second model (movement away from damaged plant); if movement away from the damaged plant is

impossible, however, the physiological reaction, as in the first model, will occur and a drop in fecundity will result.

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