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Seasonal changes in ovipositional selectivity in the monophagous leaf beetle *Zygogramma suturalis* (Coleoptera: Chrysomelidae)

Sergei Ya. REZNIK

Zoological Institute, Russian Academy of Sciences, St. Petersburg, 199034, Russia

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Abstract. Results from field samples indicate that the percentage of eggs laid by the monophagous leaf beetle, *Zygogramma suturalis* directly on the host plant (*Ambrosia artemisiifolia*) changes during the course of the season. These changes in oviposition were not associated with changes in the host specificity of larvae or adult beetles. In June–August the percentage of eggs laid on *A. artemisiifolia* was inversely correlated with *Z. suturalis* larval population density. It is speculated that high larval density deterred ovipositing females.

INTRODUCTION

This article describes seasonal changes of ovipositional selectivity in the ragweed leaf beetle, *Zygogramma suturalis* F. (Coleoptera: Chrysomelidae), which has been introduced from the USA and Canada for biological control of ragweed, *Ambrosia artemisiifolia* L. (Asteraceae), a harmful weed in Russia (Kovalev et al., 1983; Kovalev, 1989). *Z. suturalis* adults and larvae are able to feed and normally develop only on *A. artemisiifolia* and the closely related *A. psilostachya* D.C. (Reznik & Kovalev, 1989); the latter plant was absent from the sites studied here. Previously published field investigations have shown that ovipositional selectivity plays an important role in the regulation of *Z. suturalis* population density. Ovipositing females usually prefer sites with large undamaged plants. Surprisingly, up to 80% of the eggs in some samples were deposited on non-host substrata (Reznik, 1989, 1991).

It is common knowledge that phytophagous insects can significantly increase the success of their offspring by selectively laying eggs on host plants, since hatching larvae are usually incapable of travelling great distances in search of food. However, in natural conditions phytophagous insects sometimes lay a large share of their eggs on non-host plants and other substrata (May & Ahmad, 1983; Carlberg, 1984; Dennis, 1984).

In some insects ovipositional behavior tends to vary during a season. Host plant alternation, i.e. obligatory seasonal switching between hosts, is characteristic of many Aphididae (Moran, 1983, 1988; Mackenzie & Dixon, 1990) and of certain leafhoppers (Claridge & Wilson, 1978a,b). Differences in larval food suitability and female oviposition preference between the 1st and 2nd generations were also observed in oligophagous Hemiptera (Melber et al., 1981) and in Lepidoptera (Nakasuji et al., 1986). Variations in ovipositional selectivity can be found even in host-specific insects, and are considered a result of climatic influence (Kok & Mays, 1989). Little is known as yet about seasonal changes in ovipositional behavior in host-specific (particularly monophagous) insects.

MATERIALS AND METHODS

Field studies were conducted in 1983–1984 around the first introduction site of *Z. suturalis* (Stavropol' district, Russia), which has high population densities of common ragweed (mean wet phytomass, ca 300 g/m^2). Samples were obtained by randomly selecting 10 to 40 0.1 square meter plots. Two sites were studied in 1983, and one in 1984. In all sites the larval population density was high (300–1200 larvae/m^2 during population peak). In every plot the number of eggs, larvae, and adults of *Z. suturalis*, the wet weight of *A. artemisiifolia* and other plants, and the mean degree of ragweed damage (in 1983) were estimated. All plants, plant debris and ground surface were inspected for beetles, larvae and eggs, and their numbers in each substrate were individually recorded.

The mean percentage of eggs laid on ragweed was calculated by dividing the number of eggs laid on ragweed in all plots by the total number of eggs found in all substrata of the sample. Single samples were usually collected at each site every ten days, but when two samples were collected at the same site within the same ten-days period, the results were averaged. The percentage of beetles found directly on ragweed was calculated in the same manner. The proportion of ragweed in the total plant phytomass was calculated by dividing the total weight of the ragweed in the sample by the total weight of all plants. *Z. suturalis* eggs are usually laid singly, or in small batches consisting of 2–3 eggs (Reznik, 1989); each egg was therefore considered a statistical event. The method of estimating ragweed damage was described earlier (Reznik, 1991). Statistical treatment included Pearson's correlation analysis and χ^2 test.

RESULTS

In the North Caucasus, *Z. suturalis* left its hibernation sites in April–May, and began to feed and, then, to reproduce. The first oviposition period occurred in May and June. 1st generation beetles finished their development in June–July and laid eggs in July and August (Fig. 1). Field samples indicated that, except in June, the percentage of eggs laid on

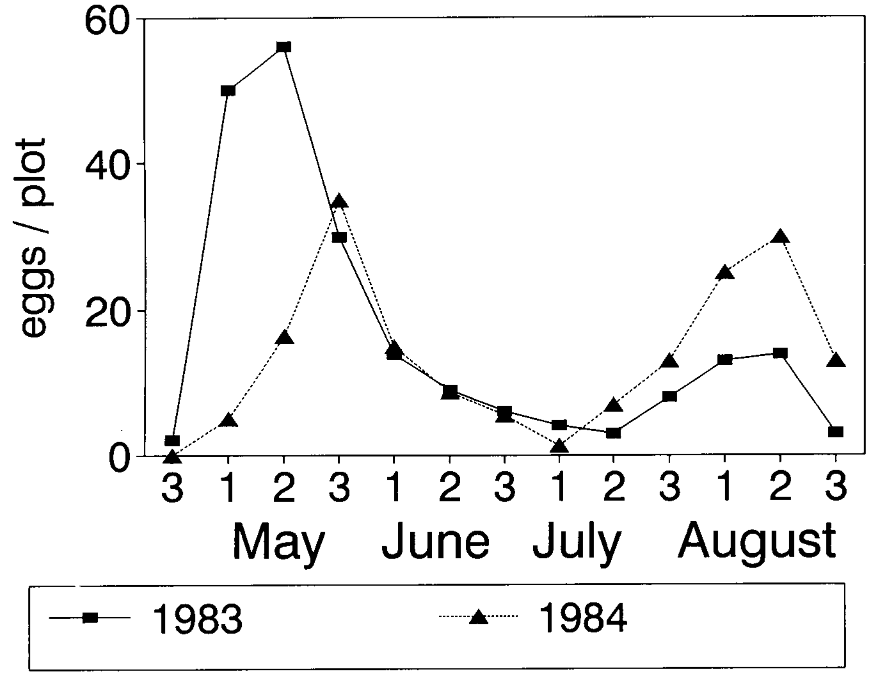

Fig. 1. Dynamics of *Z. suturalis* egg population density in 1983 and 1984. Each symbol represents the mean for ten days. Standard errors (ca 10–20% of the means) were not included, for clarity of presentation. Data for 1983 are given with means for sites 1 and 2.

ragweed was significantly higher than the percentage of ragweed phytomass in the total plant community (Table 1). Seasonal changes in the percentage of eggs laid directly on ragweed were very similar in different sites (Figs 2A,B and 3). It was apparent at all sites that at the beginning of the oviposition period eggs rarely were laid on the host plant. In all sites the percentage of eggs laid on ragweed significantly (χ^2 test) increased in the middle of May, then significantly decreased, reaching minimum in the middle of June, then increased again to 90–100% in July–August. In 1984 the percentage of eggs laid on ragweed slightly but significantly decreased in the middle of August (Fig. 3).

TABLE 1. Percentage of ragweed phytomass in total plant phytomass and percentage of eggs laid on ragweed. Significance of the difference between phytomass and egg distributions was calculated by χ^2 test.

Date	Phytomass (g : m^2)			Significance of difference	Eggs (indiv. : m^2)		
	Ragweed	Other	Ratio		Ragweed	Other	Ratio
May, 6–14	22 : 2.7	63 : 2.7	29%	$p < 0.05$	158 : 2.7	156 : 2.7	50%
June, 15	483 : 1.4	445 : 1.4	52%	n.s.	67 : 1.4	70 : 1.4	49%
July, 20	6250 : 2.8	6406 : 2.8	49%	$p < 0.001$	552 : 2.8	44 : 2.8	95%
August, 4	3300 : 1.3	3355 : 1.3	49%	$p < 0.001$	390 : 1.3	11 : 1.3	97%

Correlation analysis showed a significant negative correlation between the percentage of eggs laid on ragweed and the mean larval density (in 1983 in the 1st site $r = -0.75$, in the 2nd site $r = -0.70$, and in 1984 $r = -0.75$, all $p < 0.01$). The influence of the larval population density of *Z. suturalis* on the ovipositional selectivity of females is apparent from data from all sites, as summarized in Fig. 4. The mean rate of ragweed damage by *Z. suturalis* larvae and adults did not change considerably in June–July (Fig. 2A,B).

DISCUSSION

Our field data concerning the dynamics of egg densities accord well both with laboratory experiments in the Stavropol' district (Vinogradova & Bogdanova, 1989) and field observations in Northeastern Ohio, USA (Piper, 1975). A considerable percentage of 1st generation females enter summer-winter diapause (Vinogradova & Bogdanova, 1989), and this is why egg density during the second oviposition period is often lower than during the first one (Fig. 1).

Ovipositional selectivity in *Z. suturalis* was a stochastic but not a random process. Beetles often lay their eggs directly on the host plant, as can be expected of a monophagous beetle. According to Piper (1975), *Z. suturalis* eggs are deposited on the underside of young ragweed leaves. Our field samples indicated that ragweed leaf beetle eggs were deposited not only on ragweed, but also on other (non-host) neighboring plants, dry plant debris, and ground surface. The percentage of eggs laid directly on the host plant showed considerable seasonal changes. Piper (1975) did not observe seasonal changes, possibly due to a relatively low *Z. suturalis* population density and/or the short duration of the observation period.

Identifying the mechanisms underlying these seasonal changes seems more difficult. Seasonal changes can coincide with generational change (Claridge & Wilson, 1978a,b). In *Z. suturalis*, however, the dynamics of the percentage of eggs laid on ragweed did not

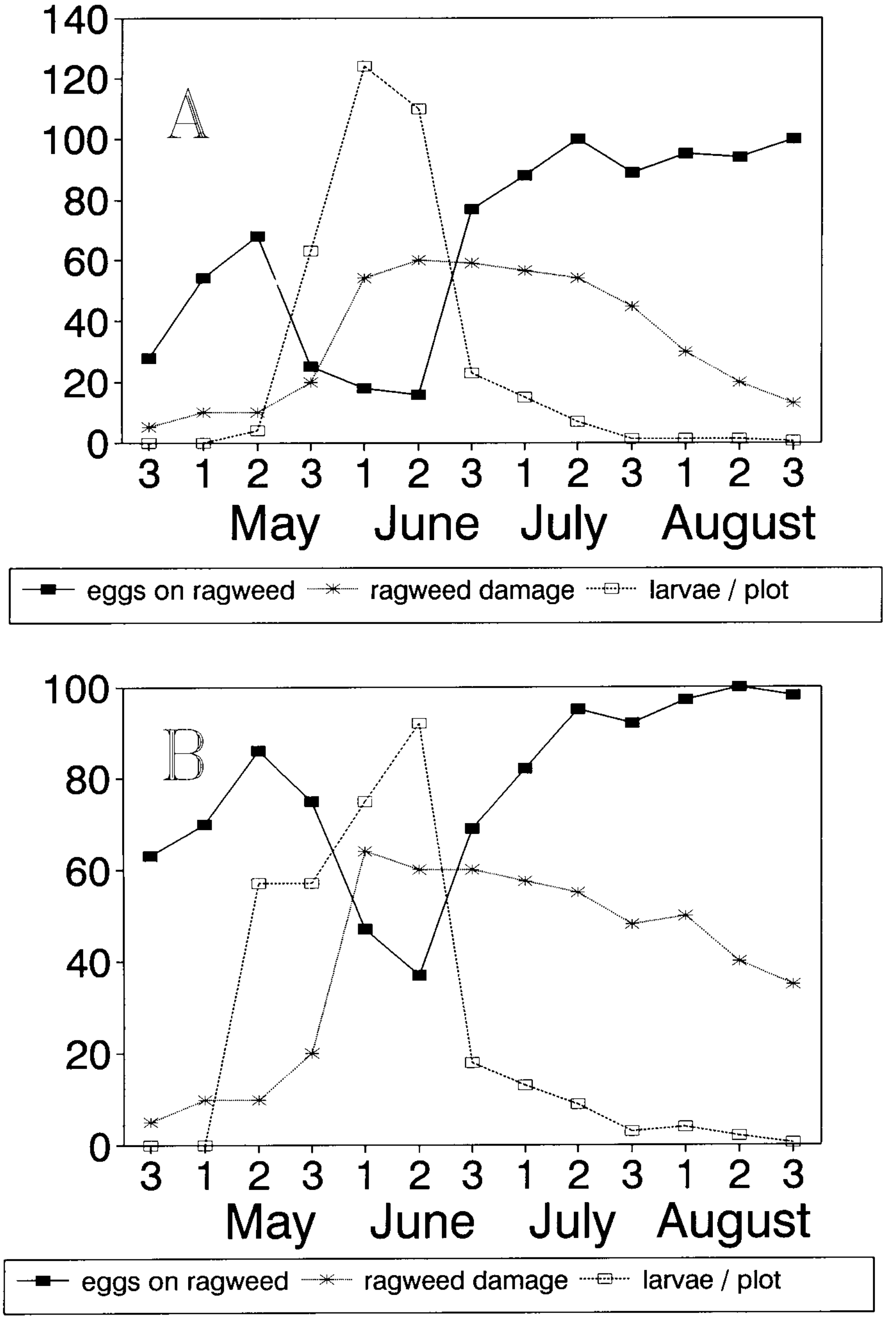

Fig. 2. Seasonal changes in the percentage of *Z. suturalis* eggs laid on ragweed, larval population density (indiv./m^2), and mean rate of ragweed damage (%) in 1983. Each symbol shows the mean for ten days. Standard errors (ca 10–30% of the means) were not included for clarity of presentation. A – site 1, B – site 2.

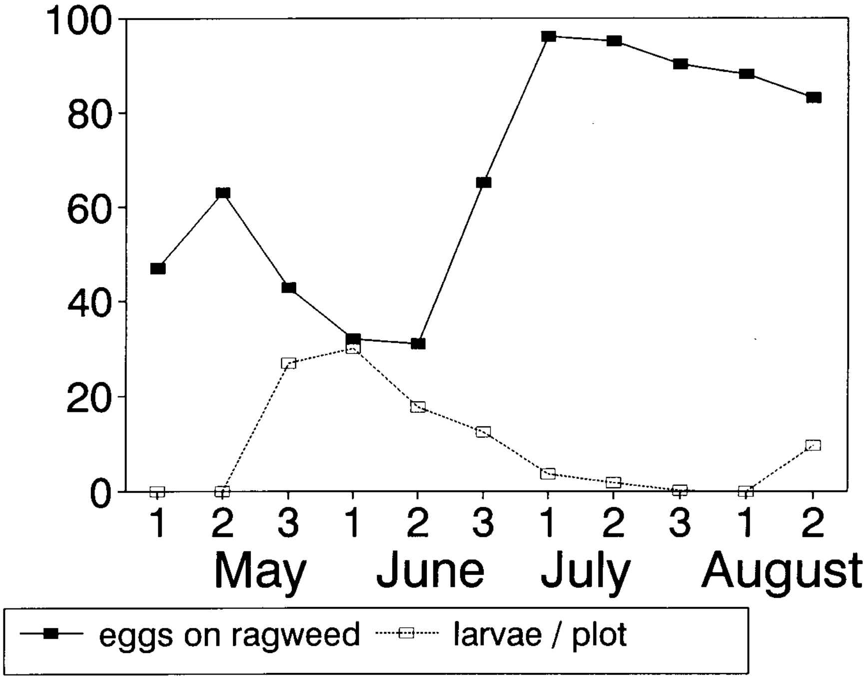

Fig. 3. Seasonal changes in the percentage of *Z. suturalis* eggs laid on ragweed, and larval population density (indiv./m^2) in 1984. Each symbol shows mean for ten days. Standard errors (ca 10–30% of the means) were not included for clarity of presentation.

correlate with generation change (comp. Figs 1, 2 and 3). Larval population density significantly correlated with the percentage of eggs laid on ragweed. In 1984, a decrease in the percentage of eggs laid on ragweed was also observed in August, during the second peak larval abundance. In 1983 there was no such decrease in August (comp. Figs 2 and 3). Note that in 1984 the second oviposition peak was almost twice as high as that in 1983 (Fig. 1), which resulted in a relatively high larval population density in August 1984.

Thus, larval density seems to have been the main factor in the decrease in the percentage of eggs laid on the host plant in June (Fig. 4). The results of this field investigation support earlier reported laboratory experiments, which showed that a high degree of feeding damage to ragweed and larval excretions deter ovipositing females (Reznik, 1989, 1991). However, Fig. 2 shows that in June–July, when the percentage of eggs laid on ragweed increased abruptly, the mean rate of damage was almost constant. These results suggests that the degree of damage plays a major role in regulating the population density (Reznik, 1991), while larval density regulates ovipositional selectivity in a strict sense (i.e., substrate choice). Leaf beetle larval secretions can now be considered not only a chemical defense, but also as intraspecific semiochemicals, i.e. larval secretions deter female oviposition and feeding (Szentesi, 1981; Raupp et al., 1986; Hilker, 1989a,b).

The decrease in the percentage of eggs laid on ragweed in June can be explained as a reaction to high larval density. In the beginning of May, when *Z. suturalis* larvae are

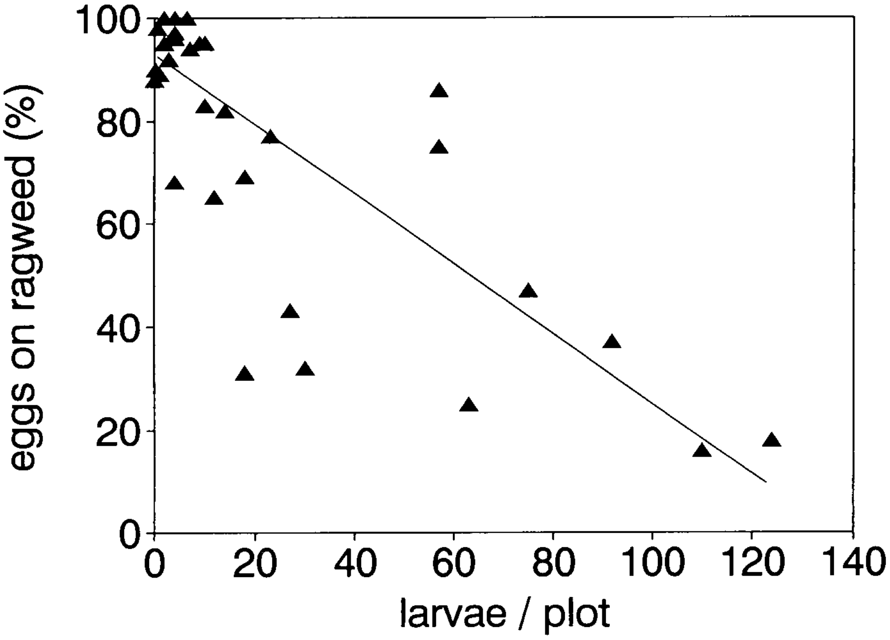

Fig. 4. Influence of *Zygogramma suturalis* larval population density on the ovipositional selectivity of females. Each symbol shows a site's mean for ten days. Only samples made after first larval hatching (the middle of May) are included. Line shows regression: $Y = 89-0.62X$, $r = -0.78$, $p < 0.001$.

absent, eggs are often also laid on non-host plants. No correlation was found between the percentage of eggs laid on ragweed and *Z. suturalis* adult or egg density (Figs 1, 2 and 3, see also Reznik, 1989). Field samples (Reznik, 1989) showed that, during this period, up to 30% of the eggs (ca 2/3 of the eggs laid on non-host plants) were laid on the underside of *Lactuca serriola* L. leaves, although the percentage of this plant in the total non-host plant phytomass was relatively low (ca 10%). The smooth and rounded leaves of young *L. serriola* plants probably make a better substrate for oviposition; in the laboratory, at least, females use them more often than those of other non-host plants (Reznik, 1989). It is possible that ragweed seedlings have less oviposition-stimulating compounds; perhaps the dimensions and/or stiffness of ragweed seedlings are not suitable for ovipositing females. Further studies are needed to verify these speculations.

It may be concluded that the percentage of eggs laid by *Z. suturalis* females directly on the host plant decreases twice during the season. In early spring (April–May), the decrease is independent of population density, while in June it is correlated with larval abundance. The mechanisms of these two decreases are apparently different.

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REFERENCES

Carlberg U. 1984: Oviposition behavior in the Australian stick insect Extatosoma tiaratum. *Experientia* **40**: 888–889.

Claridge M.F. & Wilson M.R. 1978a: Ovipositional behavior as an ecological factor in woodland canopy leafhoppers. *Entomol. Exp. Appl.* **24**: 101–109.

Claridge M.F. & Wilson M.R. 1978b: Seasonal changes and alternation of food plant preferences in oligophagous mesophyll-feeding leafhoppers. *Oecologia* **37**: 247–255.

Dennis R.H.L. 1984: Egg-laying sites of the common blue butterfly, Polyommatus icarus (Lepidoptera, Lycaenidae): the edge effect and beyond the edge. *Entomologist's Gaz.* **35**: 85–93.

Hilker M. 1989a: The regulation of the population density of phytophagous insects with special reference to "density indicators" and oviposition deterrence. *J. Appl. Entomol.* **107**: 310–317.

Hilker M. 1989b: Intra- and interspecific effects of larval secretions in some chrysomelids (Coleoptera). *Entomol. Exp. Appl.* **53**: 237–245.

Kok L.T. & Mays W.T. 1989: Comparison of the seasonal occurrence of Trichosirocalus horridus (Panzer) (Coleoptera: Curculionidae) in Virginia between 1981–83 and 1979. *J. Entomol. Sci.* **24**: 465–471.

Kovalev O.V. 1989: Dispersal of adventive plants of Ambrosiaceae tribe in Eurasia and methods of biological control of Ambrosia L. (Asteraceae). *Proc. Zool. Inst. (Leningrad)* **189**: 7–23 (in Russian, English abstr.).

Kovalev O.V., Reznik S.Ya. & Cherkashin V.N. 1983: Specific features of methods of using Zygogramma Chevr. (Coleoptera, Chrysomelidae) in biological control of ragweed. *Entomol. Obozr.* **62**: 402–408 (in Russian, English abstr.).

Mackenzie A.M. & Dixon A.F.G. 1990: Host alternation in aphids: constraint versus optimization. *Amer. Natur.* **136**: 132–134.

May M.L. & Ahmad S. 1983: Host location in the Colorado potato beetle: searching mechanisms in relation to oligophagy. In S. Ahmad (ed.): *Herbivorous Insects.* Academic Press, New York, pp. 173–199.

Melber A., Klindworth H.-G. & Schmidt G.H. 1981: Seasonal change of host plant in the arbicole bug Elasmucha grisea L. (Heteroptera: Acanthosomatidae). *J. Appl. Entomol.* **91**: 55–62.

Moran N.A. 1983: Seasonal shifts in host usage in Uroleucon gravicorne (Homoptera: Aphididae) and implications for the evolution of host alternation in aphids. *Ecol. Entomol.* **8**: 371–382.

Moran N.A. 1988: The evolution of host-plant alternation in aphids: evidence for specialization as a dead end. *Amer. Natur.* **132**: 681–706.

Nakasuji F., Kimura M. & Nishida R. 1986: Seasonal changes of oviposition-grass preference in a migrant skipper Parnara guttata (Lepidoptera: Hesperiidae). *Appl. Entomol. Zool.* **21**: 171–173.

Piper G.L. 1975: The biology and immature stages of Zygogramma suturalis (Fabricius) (Coleoptera, Chrysomelidae). *Ohio J. Sci.* **75**: 19–24.

Raupp M.J., Milan F.R., Barbosa P. & Leonhardt B.A. 1986: Methylcyclopentanoid monoterpens mediate interaction among insect herbivores. *Science* **232**: 1408–1410.

Reznik S.Ya. 1989: Oviposition behavior of the ragweed leaf beetle Zygogramma suturalis F. *Proc. Zool. Inst. (Leningrad)* **189**: 24–44 (in Russian, English abstr.).

Reznik S.Ya. 1991: The effects of feeding damage in ragweed Ambrosia artemisiifolia (Asteraceae) on populations of Zygogramma suturalis (Coleoptera, Chrysomelidae). *Oecologia* **88**: 204–210.

Reznik S.Ya. & Kovalev O.V. 1989: Feeding behavior of adults of the ragweed leaf beetle Zygogramma suturalis F. *Proc. Zool. Inst. (Leningrad)* **189**: 56–62 (in Russian, English abstr.).

Szentesi A. 1981: Antifeedant-treated potato plants as egg-laying traps for the Colorado beetle (Leptinotarsa decemlineata Say, Coleoptera, Chrysomelidae). *Acta Phytopath. Acad. Sci. Hung.* **16**: 203–209.

Vinogradova E.B. & Bogdanova T.P. 1989: Characteristics of seasonal development of Zygogramma suturalis F. *Proc. Zool. Inst. (Leningrad)* **189**: 62–75 (in Russian, English abstr.).

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