The Role of Solitary Population Waves in Efficient Suppression of Adventive Weeds by Introduced Phytophagous Insects

O. V. Kovalev and Yu. V. Tyutyunov

Zoological Institute of Russian Academy of Sciences, St. Petersburg, 199034 Russia
e-mail: kovalev@OK11495.spb.edu
Institute of Arid Zones, Southern Scientific Center of Russian Academy of Sciences, Rostov-on-Don, Russia
Research Institute of Mechanics and Applied Mathematics, Southern Federal University, Rostov-on-Don, Russia
e-mail: tyutyunov@sfedu.ru

Abstract—Successful introduction and application of phytophagous insects to control invading weeds is a complex systemic process based on formation of solitary population waves (SPW) of phytophages. Consequently, each stage from selection to release of the biological control agent should pursue the objective of the wave formation. When selecting a biological control agent one should choose species among phylogenetically young "juvenile taxa," which are capable of forming a solitary population wave upon introduction. The initial phytophage population increase, preceding the wave emergence, requires special conditions, in particular a high density of the weed in the release areas. The SPW restores the natural succession previously arrested by the weed, allowing the native plants to overgrow the weed completely.

None of the directions of classical biological control of pests has been as efficient in large territories as introduction of phytophagous insects from the native ranges of adventive plants (Hoffmann, 1995; Julien and Griffiths, 1998; Myers and Bazely, 2003; Page and Lacey, 2006; van Klinken and Raghu, 2006). Although this direction is 150 years old (Müller-Schärer and Schäffner, 2008), it still lacks a systemic approach, either to determining the factors of efficiency of biological control or to finding the most efficient agents. Success in biological control may be considered in terms of a lottery model (Myers, 1985) with unpredictable results.

In particular, the program of modern biological control considered in the review of Müller-Schärer and Schäffner (2008) and based on the works of Briese (2000) and van Klinken and Raghu (2006) includes two main stages: search for phytophages effective in biological control and selection among them of species strictly specific to the given target. It is natural that only safe species should be introduced; therefore, the most important step is selection of species by the peculiarities of their biology. Evaluation of the efficiency of a particular agent is possible only after it has been introduced. A question arises, whether success may be determined solely by preliminary evaluation of the species biology within its primary range, or the efficiency of introduced phytophages depends on a more complex systemic process. It is evident that such systemic process, in which the vast foci of adventive weeds are suppressed within the time periods impossible in the primary range of the weed, cannot be reduced to the specific biological traits of the phytophage.

Experience with successful acclimation of the ragweed leaf beetle *Zygogramma suturalis* F. (Coleoptera, Chrysomelidae) in the Old World (Kovalev and Medvedev, 1983; Cherkashin, 1985; Kovalev and Vechernin, 1986, 1989; Matishov et al., 2012; Kovalev et al., 2013) allows the routine evaluation of effectiveness of biological control to be supplemented by factors facilitating the emergence of solitary population waves (SPWs) of the phytophage (see figure). The passing of the waves of the leaf beetle in the 1980s was conducive not only to the destruction of large ragweed foci in the south of Russia and Ukraine, but also to the dispersal of this phytophage over the Black Sea coast. The long-term effect of these SPWs led to a drastic decrease in the abundance of ragweed seeds in the soil, a rise in the crop yield, and reestablishment of the vegetation succession pattern which had existed before the ragweed invasion (Kovalev and Vechernin, 1986, 1989; Kovalev et al., 2013).

The front of the solitary population wave (SPW) of the ragweed leaf beetle (Stavropol Territory).

Already in 1989, a model of the systemic process in the biological control of alien plants was suggested (Kovalev, 1989c), according to which the key factor of the weed control efficiency is the solitary population wave which destroys the adventive weed foci and determines normal succession into the state which existed before the appearance of the ragweed. The use of this concept for analysis of successful biological control campaigns has led us to the conclusion that introduction of phytophages is pointless if it does not result in a solitary population wave. Strange as it may be, the dynamics of vegetation and processes of succession still attract little attention, not only in reviews of successful biological control projects but also in attempts at modelling the underlying systems.

The Problem of Choosing Efficient Phytophages for Introduction

Some authors justly avoid using the term "efficient agent" and prefer the term "successful agent" (Julien and Griffiths, 1998). However, the term "efficient agent" is also widely used in the literature (Müller-Schärer and Schäffner, 2008). Indeed, such species of phytophagous insects are distinguished in all the successful biological control campaigns not only by their efficiency but also by the duration of control executed in the adventive weed foci.

Is it possible to explain why some phytophagous insects proved to be "efficient," i.e., were able to solve the problem of weed control? This method of comparison of the most effective species with other introduced phytophages was used by McFadyen (2000) who selected the most successful projects of control of 41 adventive weed species from the data of the *World Catalogue of Agents and Their Target Weeds* (Julien and Griffith, 1998).

We have found that in these randomly chosen projects, the majority of the species characterized as "successful" by McFadyen (Table 1) were capable of forming solitary population waves after introduction (Kovalev and Vechernin, 1986, 1989). We use the term "SPW-invaders" to distinguish such species from other introduced phytophages.

Thus, success or "efficiency" of a particular species is not solely determined by the specific traits of its biology within its native range. The formation of a solitary wave of the phytophage population density, spreading over the weed focus similar to the flame autowave, involves changes in the population dynam-

Table 1. The fraction of SPW-invaders in the total number of phytophages introduced during global biocontrol projects

Adventive weed species	Number of introduced phytophages / Number of successful biocontrol agents	Countries where introduction projects were carried out
Opuntia aurantiaca	6/1	Australia,
O. elatior	1/1	India, Indonesia
O. ficus-indica	9/3	USA (Hawaii),
O. imbricata	1/1	Australia, South Africa
O. leptocaulis	1/1	South Africa
O. littoralis	1/1	USA
O. oricola	1/1	USA
O. streptacantha	6/2	Australia
O. stricta	9/2	Australia, New Caledonia, India, Sri Lanka
O. triacantha	3/2	West India
O. tuna	3/2	Mauritius Island
O. vulgaris	4/2	Australia, India
Hypericum perforatum	11/2	Canada, USA (Hawaii), Chile, South Africa

ics of the introduced species (as compared with its biology within the native range); therefore the biological control should be assessed as a systemic process. At the same time, a considerable additional role in adventive weed suppression is played by the dynamics of vegetation associated with the passing of SPWs. By destroying the dense weed foci, the SPW of the phytophage eliminates the inhibitor species, blocking succession in the phytocenoses (Mirkin and Naumova, 2012), whereas local plants, in turn, prolong the effect of weed suppression by the phytophage.

It should be reminded that the biophysical phenomenon of soliton-like SPWs was observed at the invasion phase (Kovalev and Vechernin, 1986, 1989; Kovalev, 2013). The SPWs arise when an alien phytophagous insect is introduced into the secondary range of its food plant. The mathematical model of this phenomenon has a solution in the form of a solitary wave advancing at a constant rate (depending on the plant density) without changing its shape. Based on the Kovalev-Vechernin equations of a SPW, an equation was obtained for the population growth at the invasion phase which describes the dynamics of the biological explosion of "the critical mass," i.e., the minimum density of the invader species. This explosion accounts for the buildup of unusually high abundance in places initially colonized by a small number of insects. The high concentration of individuals is the most specific trait of the SPW distinguishing it from the common abundance waves in the primary range of the species.

It follows from the mathematical model for *Zygogramma suturalis* F. that formation of a SPW requires a certain density of insects per unit length of the wave front. At densities not reaching the maximum value of 4–5 thousand beetles per 1 m of the wave front, the wave movement will be slower. For example, at a density of 1 thousand beetles per 1 m of the wave front, observed at the late stages of the ragweed growth, the wave speed will be only 0.1 m per day, so that the wave will seem to be almost stationary. The SPW speed depends on the mass of the ragweed consumed by one beetle and on the development stage of the infested plants. Moving over the infested field, the wave leaves behind the territory completely freed of the ragweed.

As shown in the analytical review of the world experience of biological control (Kovalev, 2004b), formation of SPWs was repeatedly observed during acclimation of beneficial phytophagous insects on new continents or islands but it was not quite understood.

The phenomenon of SPWs is a universal evolutionary factor acting during expansion of invasive species (Kovalev, 2004a, 2013; Afanasieva and Amon, 2009a, 2009b). However, the ability for forming SPWs is revealed only in phylogenetically young, or "juvenile" taxa (Kovalev, 1998, 2004a, 2007). The "cenophobic" juvenile taxa represent the initial stages in the evolution of supraspecific taxa, which appear in the process of progressive evolution due to their acquiring new

morphological and biological features opening up new vistas of intensive adaptive radiation. The juvenile taxa ensure fast filling in of ecological niches during expansion into disturbed systems or during changing of biotas under the influence of climatic fluctuations. This unstable state of the genome and the ability for expansion into disturbed systems may be maintained throughout millions of years in phylogenetically young plant or animal taxa.

The juvenile taxa reflect the position of taxa during "extensive and intensive divergence," the first of the successive phases of phylogeny of supraspecific taxa in the model of Markov and Naimark (1998). In particular, this model shows that phylogenetically young taxa are distinguished by the following features: emergence of long-living and widespread species and genera; the fast growth of such expansion parameters as diversity and geographic distribution indices as well as the duration of existence of the genera; high resistance to changes in the external conditions; the prevalence of cenophobes, explerents, and patients.

The model of Kovalev-Vechernin (Kovalev, 2007) particularly emphasizes the role of juvenile taxa during expansion (invasion): only phylogenetically young taxa are capable of forming SPWs during the rapid population growth accompanying introduction of the taxon into disturbed systems.

Most insect species selected for introduction are unable to form SPWs. For instance, in the large family Chrysomelidae (Coleoptera), the ability for forming SPWs upon introduction was revealed in representatives of only two "juvenile" subfamilies, Chrysomelinae and Galerucinae (Kovalev, 2004b).

It may seem strange at first sight that phytophages in an SPW aggregate along the wave front where food is much scarcer than immediately before the front. However, this contradiction is only apparent. The movements of phytophages in the SPW are far from coordinated: each insect moves randomly, and the intensity of such movements is the higher the less "satisfied" it is with its position. However, such behavior of each insect, which tends to leave the place with insufficient food, results in the formation and advance of the wave including a great number of individuals. Such self-organized processes, in which the chaotic behavior of each individual results in ordered dynamic structures at the population level, are well known not only for insects (Kareiva and Odell, 1978) but also for

protists (Keller and Segel, 1971; Ivanitskii et al., 1991; Tyutyunov et al., 2010).

The dynamics of population processes in SPWs differs sharply from that in the primary range: the solitary waves not only never appear in the area of origin of invasive species but even cannot be triggered there experimentally (Kovalev, 2004b).

Thus, in assessing the possible efficiency of a species for biological weed control, it is necessary to take into account not only the specific traits of its biology but also its ability to form solitary waves upon introduction.

Examples from two global projects, namely suppression of the prickly pear and Saint-John's wort, are considered below (Table 1) based on the published data (Julien and Griffiths, 1998; McFadyen, 2000).

Suppression of 12 American weed species of the genus *Opuntia* (Cactaceae) was carried out in different projects using up to 9 species of insects introduced into Australia, South Africa, India, and Oceania. Biological control of weeds was achieved in all the projects as the result of using a single agent, *Cactoblastis cactorum* (Bergroth) (Lepidoptera, Pyralidae), or closely related species of the genus *Dactylopius* Costa (Homoptera, Dactylopidae), or two species from different orders simulteneously. The use of these particular species ensured full control of *Opuntia* foci in different parts of the world.

Effective results were also obtained in projects of suppression of Saint-John's wort *Hypericum perforatum* L. (Clusiaceae) in North America, Oceania, and South Africa: 11 species of insects were introduced, and the use of leaf beetles of the genus *Chrysolina* Motsch. (Coleoptera, Chrysomelidae) was successful. One of the reviews of this project (Huffaker, 1957) contains the first published photograph of the SPW taken during the dispersal of the leaf beetle *Ch. quadrigemina* (Suffrian) in California. However, this unique phenomenon was not noticed by the cited author; neither was the unusual behavior of insects commented. The specific traits of the SPW are clearly distinguished in the photograph: even at a very high density in the wave, the insects do not traverse its front in spite of lack of food within the moving wave. In the rear of the wave the food resources are almost completely destroyed.

Let us consider in greater detail each of the three components of the systemic process determining suc-

cess of the biological method: 1) the choice of the agent capable of forming SPWs; 2) suppression of the weed foci by the wave of the phytophage, and 3) consolidation of the result of biological control by the unblocked succession process.

The Taxonomic Composition of Phytophagous Insects Capable of Forming Solitary Population Waves

What insect macrotaxa include species most widely used in the world practice of biological control?

In the random sample of 41 biological control projects for which the most successful phytophages were identified (McFadyen, 2000), species capable of forming SPWs mainly belong to three orders of Holometabola: Coleoptera, Diptera, and Lepidoptera. These are the most differentiated and species-rich orders of insects.

It can be suggested that extreme abundance of taxa in these orders is related to their evolutionary ability to form SPWs during invasions into disturbed ecosystems. The juvenile taxa in SPWs reveal a high level of phenotypic variation (Kovalev, 1989b, 2013).

The remaining macrotaxa are represented in this group of phytophages by single families from the orders Homoptera and Hymenoptera. The inconsiderable role of "SPW-invaders" among the Hymenoptera is related to prevalence of other evolutionary strategies in this order.

Finally, as concerns the family level, the phytophages most widely used in biological control belong to the family Chrysomelidae and the superfamily Curculionoidea (Curculionidae, Apionidae) of the order Coleoptera, the families Pyralidae and Tortricidae of the order Lepidoptera, the family Tephritidae of the order Diptera, and the families Dactylopiidae and Psyllidae of the order Homoptera.

Dynamics of Population Processes During Invasions of Phytophages into Adventive Weed Foci

In practice, introduction of phytophages for biological control is attempted in zones of intensive infestation where the densities of the adventive plant are very high. Formation of SPWs during colonization by phytophages is possible only under such conditions, which is also confirmed by the mathematical model (Tyutyunov et al., 2013). The appearance of non-linear autostructures (population waves) may indicate a complete disruption of the cenotic milieu under the

dominance of an adventive plant in its secondary range. Adventive weeds block the succession process and create homogeneous "nidi" (Kovalev, 2004b) that facilitate formation of non-linear wave structures when phytophages are introduced. Such "nidi" resemble agrocenoses in that they are homogeneous stable systems formed by the dominant plant; such systems are never formed in the native range of the weed. Therefore, the "nidi" have a single homogeneous state necessary for emergence of an SPW when the specific phytophage is introduced from the native range.

In the section *Genetic structure of the target population and implications for biological control* (Müller-Schärer and Schäffner, 2008), the authors of the review devote great attention to the variability of the dominant plants in weed foci, hoping to reveal some possibilities for biological control.

However, we suppose that for obtaining efficient SPW, not individual variability of plants but overall homogeneity of their association in the new range is important: the more homogeneous and dense is the focus, the more likely is the SPW and the greater effect should be expected from application of the biocontrol method.

Of much greater significance may be variability in the phytophage population. Incredible as it may seem, no entomologist has ever tried to study populations of successfully introduced phytophages at the growing phase, when it would be possible to reveal the high level of variation peculiar to SPWs (Kovalev, 1989b, 2004a, 2013; Afanasieva and Amon, 2009a, 2009b, 2013). Of great interest are the mechanisms which facilitate the establishment and spread of mutations appearing in the front of the population wave of the invasive species (Tyutyunov et al., 2007; Edmonds et al., 2008; Hallatschek and Nelson, 2008; Lehe et al., 2012). The SPW creates specific conditions for macroevolutionary shifts.

Similar to the ability to form solitary waves being restricted to young "juvenile" insect taxa, the adventive plants forming the weed foci also usually belong to the most advanced families, according to the *System of Magnoliophyta* (Takhtajan, 1987). Among the 41 species of adventive weeds from 17 plant families considered by McFadyen (2000), such families as Amaranthaceae, Clusiaceae, Euphorbiaceae, Zygophyllaceae, Fabaceae, and Asteraceae may be called advanced.

Moreover, it has turned out that within their native ranges, the insects that are potential SPW-invaders are

associated only with advanced, i.e., juvenile plant taxa: mainly herbaceous plants with low cenotic activity. It should be borne in mind that the advanced plant family may also include quite a few edificator species.

Thus, there appears a possibility to search for potential SPW-invaders across the insect taxa that include the already known effective biocontrol agents.

In particular, one of the most popular groups in biological control is the superfamily Curculionoidea (Coleoptera). A detailed analysis of only one subfamily Ceutorhynchinae (out of 16 subfamilies of Curculionidae) performed by Korotyaev (2012) opens up great possibilities for search for promising biocontrol agents. The largest superfamily of beetles, Curculionoidea, comprises up to 16 families with more than 62 000 species. Such diversity is the most important biological feature of this group testifying to its exceptional evolutionary success, which is associated with phytophagy and a high level of trophic adaptation. The largest families of weevils are the most advanced branches, whereas the most primitive families are relatively small. The subfamily Ceutorhynchinae is mainly associated with herbaceous plants and includes many highly specialized phytophages. Based on extensive material, B.A. Korotyaev demonstrated for the first time such an important ecological trait of weevils as their preference for plant species with low cenotic activity. The example of the subfamily Ceutorhynchinae also makes evident the association of an insect taxon actively used in biological control with advanced groups of plants.

The third component of the systemic process in weed biological control, namely vegetation dynamics, will be considered by the example of the biological control of the ragweed by the introduced ragweed leaf beetle.

The Influence of the Ragweed Leaf Beetle on the Vegetation Dynamics in Fallow Lands

The ragweed is the strongest explerent of all the annual weeds in the south of Russia; without combined application of agrotechnical, chemical, and biological methods, none of them alone is capable of suppressing the ragweed (Ipatov et al., 1989; Kovalev, 1989a).

During the initial period of dispersal of the ragweed leaf beetle prior to the formation of the solitary wave, at low abundance of the phytophage, a special role belongs to the succession process with participation of plants blocked by the ragweed. Depending on the bur-

ied seed reserve, different plant species acquired the dominant position at the initial stages of succession in each zone of the leaf beetle dispersal. Their role in the vegetation drastically increases in the second year, when the ragweed is demolished by the leaf beetle. Abundance of plant species at the first stage of succession reveals sufficiently significant positive correlations. The onset of the first and second stages of succession under the influence of the leaf beetle proceeds with the same periodicity as it does in North America. No significant changes in the vegetation dynamics occurred in the control territory where the leaf beetle was initially released in 1979–1982 (Kovalev and Onosovskaya, 1989; Kovalev et al., 1989). Before the population buildup of the phytophage, removing the pressure of the ragweed in May–June allowed a number of spring-summer and summer species to develop actively and to complete vegetation in the same manner as they had done before the appearance of the ragweed. The influence of the leaf beetle was studied throughout several seasons, which resulted in an important conclusion that leaf beetles were highly effective in May, when the ragweed was at the seedling stage (Cherkashin, 1985). At an average density of 3 ind./m^2, the beetles destroyed 64% of seedlings, and at 9 ind./m^2, 80%. An important aspect is decrease in the ragweed seed production. A decrease in the number of seedlings, the projective cover, and height of the ragweed leads to reduction of the photosynthetically active surface of the plants. A decrease in seed production leads to fewer seedlings appearing in the next year. A decrease in seed production from year to year results in depletion of the seed reserves in the soil. For example, the upper 20-cm soil layer in the experimental plot contained 24 000 ragweed seeds per m^2 before the appearance of the leaf beetle and only 647 seeds per m^2 in 1983, whereas in 1985 only 120 and 35 ragweed seeds per m^2 were found in the fallows and in the crop rotation land, respectively (Kovalev and Vechernin, 1986). A drastic decrease in the ragweed seed reserve occurred under the influence of both the phytophage and the competing plants (Kovalev et al., 1989). The total decrease in seed production was accompanied by a decrease in the number of seeds per one ragweed plant (Table 2).

After the formation of the solitary wave and an unusually high concentration of insects (up to 5 000 ind./m^2), the ragweed is demolished in the rear of the wave. A special role in the vegetation dynamics in the fallows and the infested agrocenoses of Stavro-

Table 2. The influence of the ragweed leaf beetle on the parameters of ragweed development

Damage to ragweed, points	Parameters					
	projective cover, %	number of plants per 0.25 m^2	height of plants, cm		number of seeds per 0.25 m^2	number of seeds per plant
			June	July		
4–5	12.5	15.7	20.1	19.3	440.4	25.8
2–3.5	38.5	30.1	30.0	37.2	1570.5	59.5
0–1.5	60.0	53.0	40.0	55.0	3547.2	76.3

pol Territory belongs to the horseweed *Erigeron canadensis* L. (Asteraceae), the most widespread companion of the ragweed within its native North American range. The horseweed proved to be the most sensitive indicator of ragweed suppression by the leaf beetle in 1980–1986 (Kovalev and Onosovskaya, 1989). An upsurge of the horseweed abundance marks the SPW of the leaf beetle. The horseweed actively participates in the first stage of succession, replacing the ragweed demolished by the leaf beetle. The situation with the ragweed and the horseweed in the USA (Raynal and Bazzaz, 1975) was very close to that observed by us: the ragweed was dominant in the first year, but the horseweed formed rosettes by autumn and outstripped the ragweed by spring, becoming a dominant. This process occurs naturally in the USA, whereas in the south of Russia it is observed only when the ragweed has been weakened by the leaf beetle.

In conclusion of this brief review of systemic effects determining success of biological control of adventive plants, it is expedient to ask whether the phytocenotic method of ragweed control in the territory of the SPW formation may be considered independent.

The application of this method, referred to as the agrosteppe method, or the cenotic method of weed control (Dzybov, 2006, 2010), is limited to the area of several hectares. According to the original account (Dzybov, 2006), "the agrosteppe method, or the cenotic method of weed control, was applied in Stavropol Territory on 8 ha of fallow highly stony soil containing up to 370 ragweed plants per 1 m^2; the agrosteppe suppressed the weed almost completely in the third year (down to 3 to 5 ragweed plants per 1 m^2), and totally replaced it in the fifth year. The agrosteppe is now 25 years old and it is cenotically closed not only to this particular quarantine weed but also to all the others."

However, the cited author avoids mentioning the fact that the "agrosteppe" was founded in the immedi-

ate vicinity of the place where the permanent expedition of the Zoological Institute was working on acclimation of the ragweed leaf beetle.

Moreover, analysis of all the plots testifies to the existence of a common territory of formation of SPWs of the ragweed leaf beetle in the Stavropol upland or, more exactly, in the region of the primary release of the phytophage. The expanding range of the ragweed leaf beetle covered 20 000 ha in 1984 and as much as 300 000 ha in 1986. Therefore, the vegetation dynamics in this territory was totally determined by SPWs, rather than the "cenotic method of weed control."

CONCLUSIONS

Effective suppression of adventive weed foci by introduced phytophages is a systemic process based on the phenomenon of solitary population waves (SPWs) of the insects used as agents of biological control.

The following specific traits of population processes in the SPWs of phytophages can be distinguished.

(1) Successful weed control campaigns are characterized by the effect of fast population buildup of the phytophage: during formation of the SPW, tens of millions of insects appear within 4–6 generations (Kovalev, 2004b).

(2) An unusually fast increase in abundance in the solitary wave and unusually high densities of the introduced phytophage, unknown in its native range, ensure suppression of weed foci. However, effective phytophages usually do not form aggregations and do not reach high population densities in their native ranges.

(3) Species capable of forming SPWs and clearly distinguished by their abundance dynamics in the secondary range may not reveal this ability if special conditions of reproduction and primary buildup of the critical mass are lacking.

(4) Some species can form SPWs in weed foci without the appearance of special sites of high density (Huffaker, 1957).

(5) The solitary wave in insect populations possesses the properties of an autowave. After its passing, the weed focus undergoes an irreversible change, namely, complete destruction of weed plants, which makes the immediate passing of another wave impossible. However, the possibility of repeated passing of a solitary wave is preserved until the whole reserve of weed seeds in the soil has been depleted (Kovalev and Vechernin, 1986, 1989).

(6) The high speed of solitary waves reactivates the succession process blocked by the ragweed. This process ensures long-term control of the weed after the passing of the SPW.

(7) The inconsiderable role of local entomophages during formation of SPWs in large territories should be noted. Introduction of the ragweed leaf beetle *Z. suturalis* F. was closely connected with the problem of search for effective natural enemies of the Colorado potato beetle. All the entomophages of this beetle found in the temperate zone of North America are broad oligophages or polyphages trophically associated with ubiquitous species of the tribe Doryphorini, in particular the genus *Zygogramma*. The extreme ecological plasticity of the Colorado potato beetle and the ragweed leaf beetle and their easy adaptation to various conditions in the colonized regions are accounted for by similar evolution of these young species on the northernmost boundary of advance of Neotropical species to the Nearctic. This explains the impoverished complex of specific natural enemies of both species in the Nearctic, which includes no pathogens (viruses, bacteria, and protozoa) and few parasitoids (Kovalev and Prisny, 1989).

ACKNOWLEDGMENTS

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