

Insect Associations on Leafy Spurge in Europe: Implications for Strategies for Releases of Biological Control Agents in North America

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Abstract

Five years of observations of the insect associations exploiting leafy spurge in different habitats in Italy, Austria, Hungary and Romania, are summarized. The objective of this paper is to provide a guideline, based on field records, for the release of control agents in the proper habitat. Our observations have shown that: (a) members of an insect association feed on different parts of a target plant; (b) damage to the plant is inflicted at different growth stages at different times, thus the target plant is under stress for most of the grazing season; (c) each insect species occurs in one or more characteristic habitats in areas where plants are found. Each proposed combination of weed-feeders is a selection of species which are most frequently found in certain kinds of habitats in their native home. To avoid loss of data in studying the response of a single insect species on the target weed and to have a comparison of the effects of the single species introduction versus a multiple species introduction, two kinds of release sites are suggested: (1) Release study sites, where only one species is liberated; and (2) release control sites, where all the suitable, compatible species of the insect community, are liberated.

Introduction

Experience in biological control of weeds has shown that introduction of an insect natural enemy from a specific site into several sites, some with characteristics different from the original site where the insect was collected, can produce different levels of weed control. For example *Chrysolina quadrigemina* (Suffrian) (Coleoptera: Chrysomelidae) has been primarily responsible for maintaining the population of *Hypericum perforatum* L. (Hypericaceae) at a low level in open areas in California, but plants in the shaded areas are shunned by *C. quadrigemina*. Plants in shade are eaten by *Agrius hyperici* (Creutzer) (Coleoptera: Buprestidae), thus contributing to the overall control of St. John's wort (Frick 1974). In Hawaii *Chrysolina hyperici* (Forster) and *C. quadrigemina* were not effective in the driest sites infested by St. John's Wort, so the moth *Anaitis plagiata* L. (Lepidoptera: Geometridae), adapted to dry conditions, was released in these areas in 1967. The gall midge *Zeuxidiplosis giardi* Kieffer (Diptera: Cecidomyiidae) contributed to control of *H. perforatum* in moist situations (Andres *et al.* 1976).

If a target weed is continuously under stress for the entire vegetative season the chances for control are greater. For example, additional biotic stresses were of fundamental importance in controlling *Lantana camara* L. (Verbenaceae) in Hawaii, where 16 agents have been established to cover the long growing season and wide ecological range of the weed (Harris 1981). The population of tansy ragwort, *Senecio jacobaea* L. (Compositae), was significantly reduced at Fort Bragg, California, by action of the cinnabar, moth *Tyria jacobaea* L. (Lepidoptera: Arctiidae), whose larvae caused heavy defoliation during spring and summer, and by the flea beetle *Longitarsus jacobaeae* (Waterhouse) (Coleoptera: Chrysomelidae), whose larvae feed on the roots in winter and early spring, preventing regrowth (Hawkes and Johnson 1978). When several insect species are used against a target weed, a synergistic effect may be produced by the interaction of two or more species, thus increasing their individual effectiveness as biological control agents. For example the weevil *Neochetina eichhorniae* Warner (Coleoptera: Curculionidae) which occurs sympatrically on waterhyacinth *Eichhornia crassipes* (Martius) Solms-Laubach (Pontederiaceae), with the mite *Orthogalumna terebrantis* Wallwork (Acarina: Galumnidae) lays more eggs and feeds

more in the presence of the mites, possibly due to the release of a kairomone from waterhyacinth tissue (Delfosse 1978).

There are cases in which the introduction of a complex of biotic agents did not suppress the target weed. For example, knapweed (*Centaurea diffusa* Lamarck; Compositae) cannot be considered successfully controlled in British Columbia, although several insect species are well established (Myers 1985). The reasons for lack of success probably are: (1) asynchrony between the period of massive attack of the introduced agents and critical environmental and physiological factors affecting the weed; and (2) possibility of competition among the introduced agents. For example, Myers (1985) observed that the attack of *Urophora quadrifasciata* Meigen (Diptera: Tephritidae) was significantly lower on plants harboring larvae of by *Sphenoptera jugoslavica* Obenberger (Coleoptera: Buprestidae) in the roots. It seems that the competition from established agents can occasionally hinder or prevent the establishment of additional agents by competitive exclusion (Ehler and Hall 1982). A possible example occurred in St. Kitts during the program against puncture vine, *Tribulus cistoides* L. (Zygophyllaceae) where two weevil species, used successfully in other areas, were released. *Microlarinus lypriformis* (Wollaston) (Coleoptera: Curculionidae), a seed feeder in the larval stage, was introduced first and rapidly gave good control. When a second agent, *M. lareynii* (Jacquelin du Val), which feeds on *Tribulus* stems, was introduced, fewer flowers were available for *M. lypriformis*. Although recoveries were made, *M. lypriformis* did not persist (Bennett 1971). Another factor which may influence negatively the result of a multiple release is that early season herbivory may alter the quality of food available for insects that feed later in the season. Early season chewing insects associated with *Quercus emory* Torrey (Fagaceae), caused localized changes in the phytochemistry of trees (higher levels of condensed tannins and lower protein content), thus affecting the distribution, density, and survival of late season leaf-mining insects (Faeth 1986).

In light of these examples, we have to recognize that one of the bottlenecks in research on biological control of weeds is to identify the key species to use as biological control agents within a "complex" of natural enemies in the pre-introduction studies. To improve the chances of finding effective biological control agents it is important to study the various insect species feeding on a target weed in as many different kinds of habitats as possible. By using pre-adapted associations of natural enemies feeding on different parts of the target weed or the same part at different times, cumulative stress can be produced which adds to the probability of reducing the density of a target weed. The approach of using pre-adapted insect community in the appropriate ecological niches is to introduce the most effective natural enemies in a variety of niches on the host weed to keep it under multiple biotic pressure for the longest possible time in both the growth and dormant stages.

With the objective of identifying pre-adapted insect associations and employing them against leafy spurge in North America, field observations were made in Italy, Austria, Hungary and Romania from 1982 to 1987. The goal was to collect data which would help us better understand the role of insect associations on leafy spurge (*Euphorbia esula* L. "complex"; Euphorbiaceae) in different ecological habitats. Based on analyses of these observations we offer a guideline for the release of combinations of species or "recipes" for each of the major habitats in the weed problem area which has a counterpart area in Europe.

Insect Associations on Leafy Spurge

Methods

Field observations were made in Italy, Austria, Hungary and Romania on the insect associations feeding on *E. esula*, *E. virgata* Waldstein & Kitaibel "group", *E. cyparissias* L., *E. stepposa* Zor ex Prokhanov and *E. lucida* Waldstein & Kitaibel in three different kinds of habitats (moist open; moist shaded; and dry open). These habitats were characterized by their plant associations. Five sites were selected at S. Rossore (Italy), three in Austria, six in Hungary and four in Romania. The sites, having a range of 500 - 1500 spurge plants, were inspected at irregular intervals for 2-5 years. Attention was paid to those insects already

released as biocontrol agents against leafy spurge in North America and those selected as candidates for testing and possible release, the following species were recorded at these sites:

(a) Adults of *Aphthona flava* Guillebeau, *A. cyparissiae* (Kock), *A. abdominalis* Duftschmid and *A. czwalinae* Weise (Coleoptera: Chrysomelidae) and *Oberea erythrocephala* Schrank (Coleoptera: Cerambycidae)

(b) Galls produced by *Dasineura capsulae* Kieffer and *Bayeria capitigena* (Brems) (Diptera: Cecidomyiidae)

(c) Larvae of *Hyles euphorbiae* L. (Lepidoptera: Sphingidae), *Oxycesta geographica* L. (Lepidoptera: Noctuidae), and *Chamaesphexia crassicornis* Bertel (Lepidoptera: Sesiidae).

Results

Different insect associations were found on the same species of spurge plant in different habitats (Table 1). For example, at S. Rossore (Italy), in the dry open sites, the flea beetle *Aphthona flava* and the gall midge *D. capsulae* were more abundant on *E. esula*. In the moist open sites, *D. capsulae* was still abundant, but the companion species were *B. capitigena* and *O. erythrocephala*, instead of the flea beetle. In a moist shaded site the common species found were the gall midge *B. capitigena* and the cerambycid beetle, *O. erythrocephala*. On *E. cyparissias* plants in moist open sites the makeup of the association changed again with *O. erythrocephala* and *D. capsulae* being most common.

In a moist open site at Alland, Austria, the representative species on *E. virgata* was the midge *D. capsulae*. Whereas in a dry open site at St. Polten, Austria, the flea beetle *A. cyparissiae* was abundant on *E. cyparissias*. Whereas in a moist open situation, at Obendorf, Austria the flea beetle *A. czwalinae* was abundant on *E. esula*.

At three localities in Hungary, on plants of *E. virgata* "group" (two moist open and one dry open habitat), *O. erythrocephala*, *B. capitigena*, *D. capsulae* and *H. euphorbiae* were present. These insects were commonly found here, but never in large numbers. In a moist open site (Nadudvar), a high population of *O. erythrocephala* was found associated only with *E. esula*, although *E. virgata* plants also were present at the same site. Furthermore, adults of *A. cyparissiae* were abundant on *E. cyparissias* plants in a dry open area (Site A) near Gyor; whereas *A. czwalinae* was commonly found on *E. esula* in a moist shaded habitat (Site B) in the same area.

In Romania, larvae of *O. geographica* were abundant on *E. virgata* in a dry open site at Focsani (Site A) and larvae of *C. crassicornis* were common at the same site. Larvae of *O. geographica* were also abundant on *E. stepposa* in a dry open site at Focsani (Site B). In Braila (Site A), *O. erythrocephala* was abundant on *E. lucida* in a moist shaded site; whereas in site B of the Braila area, a dry open site, *C. crassicornis* was common on *E. virgata* "group".

Proposed Combinations or "Recipes" of Weed-feeders to be Released in North America Against Leafy Spurge

The number of possible introduction strategies for each ecological habitat is in part a function of the number of species of weed-feeders available. This relationship can be expressed as

$$C = 2^n - 1$$

where C is the number of combinations of n available species. The term (-1) is added to remove the zero combination (Ehler 1982). For example, in the dry open site at S. Rossore, Italy (Table 1) five insect species were found, therefore, we have $2^5 - 1 = 32 - 1$ different combinations of species which could be released. However, the combinations of weed-feeders proposed for each ecological habitat must also take into account the type of damage, the time of damage and the phenomenon of competitive exclusion (Ehler and Hall 1982).

Root borers, leaf feeders, and gall makers were selected to stress the leafy spurge plants. The feeding of some of these insects takes place early in the season at the start of flowering, when

Table 1. Insect associations on *Euphorbia* spp. in Europe in various habitats.¹

Species	Italy ²			Austria ³			Hungary ⁴				Romania ⁵			
	A	B	C	D	E	A	B	C	A	B	C	D	E	F
<i>Aphthona flava</i> Guillebeau (Coleoptera: Chrysomelidae)	3	1	1	1	1
<i>A. cyparissiae</i> (Kock)	3	3	1	.	3
<i>A. czwalinae</i> Weise	1	3	2	2	3	1	1	.	2	1	2	3	.	.
<i>Oberea erythrocephala</i> Schrank (Coleoptera: Cerambycidae)	1	3	3	3	.	1	1	1	2	2	1	.	.	.
<i>Bayaria capitigena</i> (Bremer) (Diptera: Cecidomyiidae)	3	3	3	1	3	3	2	.	2	2	2	.	.	.
<i>Dasineura capsulae</i> Keiffer (Diptera: Cecidomyiidae)	1	.	1	1	.	1	.	.	1	2	2	.	.	.
<i>Hyles euphorbiae</i> L. (Lepidoptera: Spingidae)	2
<i>Chamaesphacia crassicornis</i> Bertel (Lepidoptera: Sesidae)	3
<i>Oxycesta geographica</i> L. (Lepidoptera: Noctuidae)	3

1 Evaluation scale: *Aphthona* spp. (number of adults): 1 = 1-20 (rare); 2 = 21-100 (common); 3 = 200 (abundant); *O. erythrocephala* (number of adults): 1 = 1-10 (rare); 2 = 11-100 (common); 3 = 100 (abundant); *B. capitigena* and *D. capsulae* (number of galls): 1 = 1-30 (rare); 2 = 31-50 (common); 3 = 300 (abundant); *H. euphorbiae*, *O. geographica* and *C. crassicornis* (number of larvae): 1 = 1-20 (rare); 2 = 21-100 (common); 3 = 100 (abundant);
2 Italian sites: A = Site A, dry open, *E. esula*; B = Site B, moist open, *E. esula*; C = Site C, moist open, *E. esula*; D = Site D, moist shaded, *E. esula*; E = Site E, moist open, *E. cyparissias*.
3 Austrian sites: A = Alland, moist open, *E. virgata* "group"; B = St. Polten, dry open, *E. cyparissias*; C = Obendorf, moist open, *E. esula*.
4 Hungarian sites: A = Ebes, moist open, *E. virgata* "group"; B = Derecke, moist open, *E. virgata* "group"; C = Kisukasz, dry open, *E. virgata* "group"; D = Nadudvar, moist open, *E. esula*; E = Győr, dry open, *E. cyparissias*; F = Győr, moist shaded, *E. esula*.
5 Romanian sites: A = Focsani, dry open, *E. virgata* "group"; B = Focsani, dry open, *E. stepposa*; C = Braila, moist shaded, *E. lucida*; D = Braila, dry open, *E. virgata* "group".

the total of available carbohydrates in leafy spurge roots decreases to low levels (Army 1932). For each combination, the sequence of damage by the various species was considered to produce cumulative stresses to keep the target weed under pressure for the vegetative as well as part of the dormant season. To avoid competitive exclusion, (i.e., two species of insects competing for the same niche on the target plant or occasionally, two insect species sequentially occupying different niches on the same plant), insects which fed on different parts of the target plant were selected. Furthermore, selections were limited to those species which were commonly found within a community in a given habitat, because we assumed that these species were better adapted to that habitat.

Using the field data collected in Europe, we propose "recipes" on selected combinations of insects to be released against leafy spurge in specific kinds of habitats (Table 2). The combination *D. capsulae* - *A. flava* should be released in dry open sites. At S. Rossore the sequence of attack of these insects was as follows:

- (a) APRIL-MAY: Emergence of gall midge adults (*D. capsulae*) which lay eggs on the flower buds of leafy spurge. The larvae form galls and feed on the flower buds, reducing seed production of the infested plants.
- (b) JUNE-JULY: Emergence of flea beetle adults (*A. flava*) which feeds on leaves of all ages including large lower leaves, plant tips, and bracts. Heavy feeding by adults of this flea beetle significantly reduce the leaf surface.
- (c) JULY-AUGUST: The larvae of *A. flava* are found on the roots of leafy spurge, feeding either externally on small filamentous secondary roots or mining the perennial roots, and damaging the phelloderm or the phloem.

The combination *D. capsulae* - *B. capitigena* - *O. erythrocephala* seems to be adapted to moist open sites. For this association the following sequence of attack was observed at S. Rossore:

- (a) APRIL-MAY: Oviposition and appearance of larvae of the gall midge *D. capsulae* and their characteristic galls.
- (b) APRIL-OCTOBER: Emergence of the multivoltine gall midge *B. capitigena* (4-5 generations/year). As a consequence of the attack of this midge, and destruction of apical dominance of the primary stem by the midge induced gall, leafy spurge-infested plants usually produce secondary shoots which arise from below the apical tip gall of the infested stem. These secondary shoots are in turn attacked by the subsequent generation of adults of *B. capitigena*. Thus the leafy spurge plants are under continuous stress by the repeated attacks of this insect. These two gall midges might cause complementary damage to the infested leafy spurge plants. Competitive exclusion may arise if heavy attack of *B. capitigena* occurs. In such case, the number of flowers for *D. capsulae* are highly reduced.
- (c) MAY-JUNE: Adults of the cerambycid *O. erythrocephala* emerge. The feeding they do on leaves and inflorescences is of little significance, but stem lesions made by females searching for oviposition sites often cause premature withering of the inflorescences before seed formation.
- (d) JULY-SEPTEMBER: The first 3-4 instars of *O. erythrocephala* larvae mine the stem. Often infested stems die by the end of July. The last instar larvae feed in the root crown and in the upper part of the main root. Heavy attack by this insect may reduce the number of flowering stems. According to Schroeder (1980) in a locality near Vienna in 1977 over 90% of small *E. cyparissias* plants were infested with larvae of *O. erythrocephala* and in 1978 the number of flowering plants was decreased by 85%.

The combination of *B. capitigena* and *O. erythrocephala* may be used in moist shaded sites with the following sequence of attack:

Table 2. Proposed combinations or "recipes" of insects of European origin for biological control of leafy spurge in North America. These recipes were prepared by selecting those species better adapted for specific habitats.

Country Habitat	Insect species ¹							
	Dc	Bc	Af	Ac	Oe	He	Cc	Og
Italy								
Dry open	+		+					
Moist open	+	+			+			
Moist shaded		+			+			
Austria								
Dry open	+			+				
Moist open		+			+			
Hungary								
Moist open	+	+			+			
Dry open	+				+	+		
Romania								
Dry open							+	+

¹ Dc = *Dasineura capsulae*; Bc = *Bayeria capitigena*; Af = *Aphthona flava*; Ac = *Aphthona cyparissiae*; Ac = *Aphthona czwalinae*; Oe = *Oberea erythrocephala*; He = *Hyles euphorbiae*; Cc = *Chamaesphexia crassicornis*; Og = *Oxycesta geographica*.

(a) APRIL-OCTOBER: Damage by *B. capitigena*

(b) JUNE-SEPTEMBER: Damage by *O. erythrocephala*

Based on observations made in Austria, the combination of *D. capsulae* and *A. cyparissiae* may be used in dry open sites. These two insects evoke the same damage pattern as *D. capsulae* and *A. flava*. On the other hand, the combination *B. capitigena*-*A. czwalinae* seems more adapted to moist open sites.

Data collected in Hungary suggest the combination of *D. capsulae*, *B. capitigena*, *O. erythrocephala* can be used in moist open sites with the following sequence of feeding and damage:

(a) APRIL-MAY: Gall formation and larval feeding by *D. capsulae*, which reduces seed production of leafy spurge.

(b) APRIL-OCTOBER: Gall formation and larval feeding by several generations of *B. capitigena*, which keep leafy spurge plants under pressure for the whole vegetative season.

(c) JUNE-SEPTEMBER: Feeding of both adults and larvae of *O. erythrocephala*.

The combination *D. capsulae* - *O. erythrocephala* - *Hyles euphorbiae* appears suitable in a dry open situation. The pattern of attack of this "recipe" starts with the action of the gall midge *D. capsulae* on flower buds in April and May, followed by adult feeding activity of *O. erythrocephala* in June and July, voracious feeding on the foliage by the larvae of *H. euphorbiae* from June to August, and stress on the root system by *O. erythrocephala* larvae from June to September.

From the data collected in Romania the combination *O. geographica* and *C. crassicornis* is proposed for dry open sites, with the following sequence of feeding damage expected:

(a) MAY-JUNE: Feeding by *O. geographica* larvae, which destroy the inflorescences and foliage of leafy spurge.

JULY-NOVEMBER: *C. crassicornis* larvae feed and destroy the roots of its host plant.

Discussion

The approach of the "pre-adapted insect association in the proper niche" suggests a plan of release which does not focus or depend on a single weed-feeding species, but on a combination of weed feeders, each well adapted to a particular ecological niche on a host plant growing in a particular habitat. The advantage of using a combination of biotic agents is that different species of natural enemies damage different parts of the plant simultaneously, or the same part of the plant is damaged at different times, extending the stress over the active growing stage of the target weed.

To utilize fully the insect association release concept, it is necessary to characterize, in the pre-introduction phase, the various habitats throughout the range of weed by collecting ecological data such as species or variety of the target weed, density, vegetative community, type of soil and climate. These data are important in selecting the right combination or combinations of biotic agents to use against the target weeds. For example, leafy spurge (*E. esula* "complex") in North America possesses a broad range of diverse habitats, from xeric to subhumid and from subtropic to subarctic (Best *et al* 1980). This great variability of habitats constrains us to collect the best mix of natural enemies for each habitat where the weed is a problem.

During the initial phases of a post release study of a new introduction, a loss of ecological information would occur if more than one species was introduced at the same site. To avoid this "release study sites", where a single species of the insect association would be introduced and a "release control sites", where the appropriate "combinations" of natural enemies will be released should be established. The data collected in the "release study sites" would demonstrate the impact of a single species on the weed while the "release control sites" would demonstrate the impact of the insect association on the weed and an estimate of the time to suppress it, if the community is effective as a control method.

To maximize the speed of control, the following steps are proposed:

- (a) Characterize the more important ecological habitats within the weed problem area;
- (b) Study the natural enemies associated with the target weed and characterize the various ecological habitats where they are indigenous;
- (c) Collect and analyze the population data on the natural enemies and their host plants; these data are considered critical for assessment of the potential biological control agents, before introduction and for their effectiveness after introduction (Cock 1986).
- (d) Introduce single species in "release study sites";
- (e) Introduce the association of recommended, host-specific species in "release control sites"; and
- (f) Evaluate the impact of the introduced agents in both single species and multiple spp. release sites.

Until enough studies are made on the population dynamics of selected biological control agents and their host plants, it is unlikely that biological control will develop into a truly predictive science. In classical biological control, the prime objective is suppression of populations of alien weeds, and at present this is generally considered a long-term process.

The aim of the release of multiple species of an insect association which co-exists in its indigenous area is to produce the same association for abatement of a weed problem in a shorter amount of time.

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