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Biological control of leafy spurge in North America

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I. Introduction

Biological control of weeds is the deliberate use of natural enemies to reduce the density of a target weed to below an economic threshold. Eradication has never been achieved through biological control and indeed usually a residual population of the weed is required to maintain the control organism.

In classical biological control one or more organisms, usually insects or pathogens, from another part of the world are established on the weed. They then seek out, feed and reproduce on the weed to destroy a portion of the seeds, leaves or roots. This imposes stress on the weed but usually does not kill it unless supplemented by other stresses from the climate, soil, competing vegetation or other natural enemies. Thus, successful biological control often involves the use of several natural enemies, although the number will depend on the level of other stresses on the weed.

Most plants are subject to attack by a large number of insect and pathogen species, but only those specific to the weed can be used for biological control. The procedures for determining the host range of candidate agents are discussed by Harris and Zwölfer (38), Zwölfer and Harris (101) and Wapshere (96). The testing represents about a third of the total cost of \$2 million for controlling a weed biologically (35); however, in contrast to other methods of weed control, once the agent is established and distributed, there is little or no continuing cost.

The control of St. Johnswort (*Hypericum perforatum* L.) in western North America with the beetle *Chrysolina quadrigemina* (Suffr.) (46) is a good example of what can be achieved with classical biological control. This weed, like leafy spurge, is an introduced herbaceous perennial that before its biological control infested over 0.8 million ha in California, lowering land values by two-thirds (46). Biological control has reduced this weed to a minor entity in California and most of western North America. An example of using a pathogen is the control of skeletonweed (*Chondrilla juncea* L.) in Australia with the rust *Puccinia chondrillina* Bubak & Syd. (17).

Inundative biological control involves the periodic application of an organism, usually a pathogen, as a biological herbicide that achieves temporary control in the treated area. Indigenous pathogens that normally do not increase sufficiently to damage their weed hosts can be used, so that the method is amenable to the control of native weeds for which there are no suitable agents in other parts of the world. The use of *Colletotrichum gloeosporioides* (Penz.) Sacc. f. sp. *aeschynomene* for the control of northern jointvetch (*Aeschynomene virginica* (L.) B.S.P.) in rice grown in the United States is an example of this type of biological control (89). Similarly for insects, the use of laboratory-reared moths (*Bactra verutana* Zell.) to augment field populations for the biological control of purple nutsedge (*Cyperus rotundus* L.) in cotton was developed by Frick and Chandler (27). Inundative biocontrol has a continuing application and material cost. Therefore, for the control of an introduced weed on low-value land the preference is for classical biological control.

Spurge control can also be achieved through managed grazing with sheep (49); but grazing, the use, of competitive crops, and crop rotation are matters of management and are not considered further here.

II. Conflict of interest

In most biological control of weeds programs there are conflicts of interest that must be resolved before any agents can be released. Leafy spurge is no exception.

The most obvious potential conflict of interest in the economically important spurge *Euphorbia pulcherrima* Willd., or poinsettia, with a value of \$54,000,000/year as a Christmas pot plant (92). Fortunately this is not a serious difficulty since poinsettia has been toxic to all the European leafy spurge insects that have been tested against it.

E. antisyphilitica Zucc. (Candelilla plant) is the source of a high-quality wax that is the basis of a 1,000,000/year (93) cottage industry in northern Mexico. However, it is a tough xerophyte with only a few transient succulent leaves, which makes it an unlikely host for most leafy spurge insects.

Several annual spurges (mainly *E. micromera* Boiss. ex Englm.) are grazed by sheep and goats in the northern Sonora; however, these species are also listed as weeds in cotton (57) and so are a mixed blessing. The tree palo amarillo (*E. fulva* Stapf.) is a potentially exploitable source of rubber in central and southern Mexico (58), but both its form and location render it virtually immune from agents introduced for the biological control of leafy spurge.

Calvin (14, 15) suggested that *E. lathyris* (caper spurge) is the foremost candidate for the development of a renewable oil resource in the United States. This is a problem as *E. lathyris* is acceptable to many leafy spurge insects. Furthermore, it is difficult to compare current losses that are increasing yearly against unquantified and potential future benefits. Several non-*Euphorbia* plants are also being investigated for latex and rubber production in the United States (48, 68), and if one of these rather than *E. lathyris* is adopted commercially the conflict of interest disappears.

The conflict of interest was heightened and took a new twist in 1980 when Calvin (*in litt.*) stated that leafy spurge is a potentially valuable crop for oil and sugar production and so should not be controlled biologically. If leafy spurge is used as a commercial crop, one unfortunate consequence will be that escapes will increase its incidence as a weed in forage. Leafy spurge is presently so aggressive and difficult to control in pastures that any increase would be alarming, particularly as there are alternative oil and sugar crops.

Many ecologists regard the possibility of damage to native spurges by an introduced agent as a serious detraction to biological control. They express concern that some native plants would be reduced and that rare species might be exterminated. Biological control agents have sometimes attacked common native plants that are closely related to their weedy host, a capacity previously indicated by the feeding tests. There is no record of a biological control agent eradicating a plant, and this is unlikely to occur since the impact of the agent decreases with the scarcity of its host. The number of niches available for specialized insects on a plant species largely depends on its abundance and architecture. On native plants these are likely to be filled by native insects whose presence tends to resist the exploitation of the plant by an introduced insect. Thus, crop species introduced from another country or those with a greatly expanded geographical range are at greater risk. In either case, it is a matter of weighing the economic and ecological costs and benefits before an introduction is made.

III. Insects that attack the genus Euphorbia

Non-American insects recorded from *Euphorbia* species in the literature or found in surveys for biocontrol agents are listed in Table 1. Both the literature and North American-sponsored surveys have emphasized western Europe, so organisms attacking *E. cyparissias*, which is of Mediterranean origin, are well represented. The *E. esula-E. virgata* complex is of Caucasian origin, a region that is less entomologically known than western Europe and so far not surveyed specifically for spurge insects. Undoubtedly, a survey in this region would increase the number of species on the list, as new records are still being found in western Europe.

For example, the rearing of the weevil *Neoplinthus tigratus* Rossi from a leafy spurge root infested with *Oberea* larvae was the first host record for this species (Rizza and Pecora, *in litt.* 1979). Similarly, the rearing of large numbers of the cerambycid *Vadonia*

bisignatus Brille from *Euphorbia velenouski* Bornm, in Greece, was also a first host record (Schroeder unpublished).

The list of non-American insects that attack spurge includes 131 species. Some of these insects have broad host ranges and are obviously unsuitable as biological control agents, but others on the list show a host range restricted to the genus *Euphorbia* and occasionally a single record on a plant species in an unrelated family. The host records from unrelated plants are probably in error and warrant investigation. For example, the lace bug *Oncochila simplex* (Herrich-Schaeffer), whose real host plants are *Euphorbia cyparissias* and *E. esula*, was recorded on *Thymus* by Drake and Ruhoff (20). Also, a record by Freber (in Douglas and Scott (19) that the insect was found "in sandy places under *Senecio jacobaea*" worked its way into the literature with S. *jacobaea* as a host plant. The insect did not survive on either of these plants in laboratory feeding tests (Pecora and Rizza *in litt.* 1980).

About three-fourths of the insects that feed on *Euphorbia* are restricted to the genus, while on an architecturally similar plant, *Solidago*, at least three-fourths of the species that feed on it attack other plant genera as well (Zwölfer & Harris, unpublished). Since these plants offer similar niches, the difference in the host ranges seems to depend on the toxic latex found in the spurges that makes their exploitation by a nonspecialized insect difficult.

A difference in toxins and hence insect enemies may be the reason that *E. esula* and *E. virgata* occur in mixed stands in eastern Austria, although the plants are morphologically and ecologically similar. Thus, *E. esula* is heavily attacked by the root boring moth *Chamaesphecia tenthrediniformis* D. & S., but it does not oviposit on adjacent plants of *E. virgata*. In the laboratory, newly hatched larvae of *C. tenthrediniformis* became paralyzed on contact with a small amount of *E. × pseudovirgata* latex but bored readily into stems of *E. esula*.

The concept of chemical differences between the latex and toxins of various spurges is also supported by the results of surveys for insects on leafy spurge in Canada. These surveys have revealed no specialized native spurge insects that accept leafy spurge.

Almost one-third of the insects in Table 1 are in the Chrysomelidae genus *Aphthona*. Most *Aphthona* species are associated with *Euphorbia*, although a few species have specialized on genera in other plant families, such as *Iris* (63). The genus *Aphthona* is also found in north and central America, with 46 species listed by Wilcox (97). There is little host plant information on the American species, although several of the polyphagous species include *Euphorbia* in their host range. It is suspected that a survey of perennial native spurges, particularly those in central America, would provide host records for many of the species. If the American *Aphthona* have diversified on native *Euphorbia* species their presence in this niche will tend to block its utilization by introduced *Aphthona*.

In North America a great many insects have been collected from leafy and cypress spurge but most were nectar and pollen feeders or used spurge as a place to rest. Some polyphagous leafhoppers and Lepidoptera feed on leafy spurge but do little damage to it.

Species	Host plants,*	Part damaged	Reference
ACARINA			
ERIOPHYIDAE			
Eriophyes euphorbiae Nal.	2	Foliage	13, 80
INSECTA			
HOMOPTERA: APHIDAE			
Acyrthosiphon cyparissiae Koch	1, 2, 4, 7	Foliage	23, 43
(Macrosiphum cyparissiae Koch)			
(Mirotarsus cyparissiae Koch)			
A. cyparissiae spp. propinquum Mordv.	1, 2, 4	Foliage	23, 43
A. cyparissiae ssp. turkestanicum Nevsky	3	Foliage	23
A. euphorbiae CB	1, 5	Foliage	23
(A. euphorbiae euphorbiae Börner)	E. platyphyllos		
A. neerlandicum HRL	1	Foliage	23
(A. euphorbiae neerlandicum HRL)	E. epithymoides		
	(E. polychroma)		
Aphis asclepiadis Fitch	Polyphagous	Foliage	24
A. esulae CB	1, 2	Foliage	11
(Pergandeia esulae CB)			
A. euphorbiae Kltb.)	2, 3, 4	Foliage	11, 62, 87
(Pergandeia euphorbiae Kltb.)			
A. gerardianae Mordv.	4	Foliage	11
(Pergandeia gerardianae Mordv.)			
A. gossypii Glov.	Polyphagous	Foliage	24
(Cerosipha gossypii Glov.)			
A. paludicola HRL	5	Foliage	11
(Pergandeia palustris CB)			
Macrosiphum (Sitobion) adgnatum	E. inaequilatera,		
Müller	E. pubescens	Foliage	65, 78
<i>M. amygdaloides</i> Theob.	Polyphagous	Foliage	11
<i>M. euphorbiae</i> Thomas	Polyphagous	Foliage	55, 61
(<i>M. euphorbicola</i> Thomas)			
(M. solanifolii Ashm.)			
M. euphorbiellum Theob.	7	Foliage	61
M. inexpectatum Leclant	E. hyberna ssp. insularis	Foliage	55
Macrosiphum meixneri CB	E. villosa (E. austriaca)	Foliage	11
Myzus persicae Sulz.	Polyphagous	Foliage	11
Pemphigus brevicornis Hart.	Polyphagous	Foliage	Stoetzel (<i>in litt</i> .)
Smynthurodes betae Westw. (S. phaseoli Pass.)	Polyphagous	Roots	11

Table 1. Non-American insects and mites on the genus Euphorbia.

HETEROPTERA: COREIDAE

Dicranocephalus albipes F.	Euphorbia spp.		Kovalev (<i>in litt</i> .)
D. agilis Scop.	2, 6, E. parlandica	Fruits	86
D. medius Mul. & Ray	1, 7		86
HETEROPTERA: TINGIDAE			
Oncochila scapularis Fieber	4		95
<i>O. simplex</i> HS.	Euphorbia spp.	Foliage	95
HETEROPTERA: MIRIDAE			
Paredrocoris pectoralis Reub.	Euphorbia spp.		Kovalev (<i>in litt</i> .)
LEPIDOPTERA: NOCTUIDAE			
Acronicta abscondita Tr.	Polyphagous		9
A. euphorbiae F.	Polyphagous		9
A. rumicis L.	Polyphagous		9
Agrotis corticea Schiff.	Polyphagous		9
A. cursoria Hufn.	Polyphagous		9
<i>A. fugax</i> Tr.	2, Zea mays		9
<i>A. lucipeta</i> F.	Euphorbia,		9
	Tussilago,		
	Petasites		
Oxycesta geographica F.	2, Linaria		9
Simyra nervosa F.	Euphorbia, Rumex		9
<i>S. dentinosa</i> F.	4	Foliage	Dunn (<i>in litt</i> .)
<i>Xylena exoleta</i> L.	Polyphagous		84
LEPIDOPTERA: TORTRICIDAE			
Acrolita subsequana (HS.)	6, E. biumbellata,	Seeds	12, 26, 32
	E. portlandica		
Apterona crenulella Brd.	Polyphagous		40
Clepsis spectrana Tr.	Polyphagous		32
(C. costana F.)			
C. strigana Hb.	Polyphagous	Foliage	32
Cnephasia chrysantheana Dup.	Polyphagous	Foliage	32
<i>C. virgaureana</i> Tr.	Polyphagous	Foliage	40
Cnephasiella incertana Tr.	Polyphagous	Foliage	40
Lobesia euphorbiana Frr.	Euphorbia spp.	Foliage & shoots	32
L. occidentis Falk	E. amygdaloides	Foliage & shoots	12
Spilonota ocellana Fab.	Polyphagous	Foliage	12

LEPIDOPTERA: AEGERIIDAE

LEI IDOI TERA, AEGERIIDAE			
Chamaespheca astatiformis HS.	2, Linaria	Roots	77
C. bibioniformis Esp.	4	Roots	40
C. empiformis Esp.	2	Roots	67
C. hungarica Tomala	E. lucida	Roots	Issekutz (loc. cit. 76)
C. leucomeleana Zell.	2	Roots	40
C. leucopsiformis Esp.	2	Roots	76
C. palustris Kautz	5	Roots	76
C. stelidiformis Frr.	E. polychroma	Roots	76
C. tenthrediniformis D.& S.	1	Roots	67
LEPIDOPTERA: GEOMETRIDAE			
Biston fiduciarius Anker	Euphorbia spp.	Foliage	40
Minoa murinata Scop.	Euphorbia spp.	Foliage	40
LEPIDOPTERA: SPHINGIDAE			
Hyles euphorbiae L.	Euphorbia spp.	Foliage	37
<i>H. gallii</i> Rott.	<i>Epilobium</i> , Galium	Foliage	9, 84
LEPIDOPTERA: LASIOCAMPIDAE			
	Euphorbia?		
Malacosoma castrensis L.	Five <i>Euphorbia</i> spp., and kohlrabi in tests	Foliage	Zwölfer (<i>in litt</i> .)
LEPIDOPTERA: ARCTIIDAE			
<i>Actia hebe</i> L.	Polyphagous	Foliage	9
LEPIDOPTERA: NEPTICULIDAE			
Nepticula euphorbiella Stt.	E. dendroides,	Leaf Miner	41
N. jubae Wlsgh.	Euphorbia	Leaf Miner	41
N. tergestina Klim.	Euphorbia	Leaf Miner	41
HYMENOPTERA: TENTHREDINIDA	E		
Macrophya annulata Geoffr.	Euphorbia spp.	Foliage	8
Tenthredo solitaria Scop.	2	Foliage & Flowers	56
HYMENOPTERA: EURYTOMIDAE			
Eurytoma euphorbiae Zerova	3	Seeds	98
<i>E. bajarii</i> Erd.	3	Seeds or parasite of <i>E. euphorbiae</i>	98
DIPTERA: ANTHOMYIIDAE			
Pegomya argyrocephala Meigen	E. amydaloides	Root gall	39
P. transversaloides Schnabl	2, 3, <i>E. lucida</i>	Root gall	Michelsen (<i>in litt</i> .)
DIPTERA: AGROMYZIDAE			
Liriomyza cyparissiae Groschke	Euphorbia	Leaf Miner	39
L. esulae Hd.	Euphorbia	Leaf Miner	39

	F 1 1 .	T C.M	20
L. myrsinitae Hg.	Euphorbia	Leaf Miner	39
L. pascuum Mh.	Euphorbia	Leaf Miner	39
<i>L. strigata</i> Mg.	Polyphagous	Leaf Miner	39
<i>Melanagromyza euphorbiae</i> Hd.	Euphorbia	Leaf Miner	39
Phytomyza atricornis Mg.	Polyphagous	Leaf Miner	39
DIPTERA: CECIDOMYIIDAE	_		
Bayeria capitigena Bremi	2	Bud Gall	13, 80
Dasineura capsulae Kieff.	Euphorbia spp.	Flower & Fruit Gall	13, 80
D. loewi Mik.	1, 2, 4	Flower Gall	13, 80, 81
D. schulzei Rübs.	5, E. lucida		81
D. subpatula Bremi	1	Shoot Gall	13, 80
Macrolabis lutea Rübs.	2	Shoot Gall	80
COLEOPTERA: CERAMBYCIDAE			
Oberea euphorbiae Germ.	5	Roots	18
O. erythrocephala Schrank	1, 2, 3	Roots	83
Vadonia bissignata Brull.	E. velenovskyi	Roots	Schroeder
COLEOPTERA: CHRYSOMELIDAE			
Aphthona abdominalis (Duft.)	2, and five other <i>Euphorbia</i> spp., <i>Linum</i> ?	Roots	59
A. aenomicans All.	1, Linum	Roots	59
A. alexander Ber & Rap.	Euphorbia sp.	Roots	59
A. argentinae Bryant	E. portulacoides	Roots	59
A. atrovirens Forst.	2, Helianthemum?	Roots	59
	Linum?		
A. bonvouloiri All.	Euphorbia sp.	Roots	59
A. cyanella (Redt.)	2, and two other <i>Euphorbia</i> spp.	Roots	59
A. cyparissiae (Koch)	1, 2, 3 and two other <i>Euphorbia</i> spp.	Roots	59
A. czwalinae Weise	1, 2, 3, 4	Roots	59
A. delicatula Foudr.	2, and two other <i>Euphorbia</i> spp.	Roots	59
A. depressa All.	Four <i>Euphorbia</i> spp.	Roots	59
<i>A. euphorbiae</i> (Schrank)	Polyphagous	Roots	59
A. <i>flava</i> Guill.	2	Roots	59
<i>A. flaviceps</i> All.	6, Linum	Roots	59
A. foundrasi Jac.	<i>Euphorbia</i> sp.	Roots	59
11. journar ast out.	Phyllanthus, Linum	10005	07
A. gracilis Fald.	Euphorbia	Roots	Kovalev (<i>in litt</i> .)
A. herbigrada Curt.	2, Campanula	Roots	59
	Helianthemum		
	110000000000000000000000000000000000000		

A. illigeri Bedel	Five Euphorbia spp.	Roots	59
A. jacuta Ogl.	Euphorbia	Roots	Kovalev (<i>in litt</i> .)
A. janthina All.	E. helioscopia	Roots	59
A. lacertosa Ross.	1, 2, 3 and three other Euphorbia spp.	Roots	59
A. laevissima Woll.	E. tuckeyana	Roots	59
A. lutescens (Gyll.)	Polyphagous	Roots	59
A. mohr Warch.	E. szovitsii	Roots	59
A. nigrilabris Duv.	E. hirta	Roots	59
A. nigriscutis Foudr.	1, 2 and two other <i>Euphorbia</i> spp.	Roots	59
A. ovatus Foudr.	1, 2, 3 and eight other <i>Euphorbia</i> spp.	Roots	59
A. paivana Woll.	Three Euphorbia spp.	Roots	59
A. perrisi All.	Three Euphorbia spp.	Roots	59
A. poupillieri All.	Two Euphorbia spp.	Roots	59
A. punctiventris Rey	E. characias	Roots	59
A. pygmaea Kuts.	1, 2 and three other <i>Euphorbia</i> spp.	Roots	59
A. sajatica Ogl.	Euphorbia	Roots	Kovalev (<i>in litt</i> .)
A. sarmatica Ogl.	Euphorbia	Roots	Kovalev (<i>in litt</i> .)
A. stussineri Weise	Euphorbia	Roots	59
A. tolli Ogl.	Euphorbia	Roots	Kovalev (<i>in litt</i> .)
A. variolosa Foudr.	E. dulcis	Roots	59
A. vaulogeri Pic.	E. pubescens	Roots	59
A. veitchi Bryant	E. chamissonis	Roots	59
A. venustula Kuts.	2, 3 and five other <i>Euphorbia</i> spp.	Roots	59
A. violaceae (Koch)	Polyphagous?	Roots	59
COLEOPTERA: CURCULIONIDAE			
Acalles rolleti Germ.	E. dendroides	Stem	44
Neoplinthus tigratus Rossi	1	Roots	Rizza & Pecora (<i>in litt.</i> , 1980)

*Host plant: 1. E. esula 2. E. cyparissias 3. E. virgata

4. E. seguieriana

5. E. palustris

6. E. paralias

7. E. amygdaloides

IV. Fungi that attack the genus Euphorbia

Fungi recorded on *Euphorbia* species are listed in Table 2. Little is known about the biology of these fungi except for some rusts, which have economic plants as their alternate host. These heteroecious rusts would not be considered as biocontrol agents it their alternate hosts were economic or cultivated plant species. In North America both leafy and cypress spurge are attacked by a rust of European origin, *Uromyces striatus* Schroet., that alternates on alfalfa and clover (71). It reduces the thriftiness of individual spurge plants but has little effect on stand density. Autoecious rusts, such as *Melampsora euphorbiae* (Schub.) Cast., *Uromyces scutellatus* (Pers.) Lév. and *Endophyllum* species, are possible biocontrol agents for North American leafy spurge. Some of the other fungi that attack leafy spurge may be potential candidates as biological herbicides. European pathogens on leafy spurge provide a large resource of potential biological control agents and very little effort has been directed towards their use.

V. Taxa and origin of leafy spurge in North America

It appears that there have been a number of leafy spurge introductions into North America (21). Dunn and Radcliffe-Smith (22), in 30 herbarium sheets from 12 herbaria, found five taxa and McCarthy (60) reported a sixth from Montana. Radcliffe-Smith (79) in this volume has recognized 20 taxa of leafy spurge in North America. There are also two taxa of cypress spurge (64). It remains to be determined to what extent insects and pathogens discriminate between them. Similarly, it has to be determined if some spurges are more easily controlled with herbicides than others and how they differ ecologically. A study by Baker and Arneklen (5) indicated that the differences may be important. Also, it is clear that for biological control, treating all leafy spurges as *E. esula* has resulted in a considerable waste of time and effort.

The number of agents shared by different taxa of spurge are likely to reflect the closeness of their relationship. Thus, it is of interest that in the treatment of the genus *Euphorbia* by Prokhanov (77) *E. cyparissias* and *E. virgata* are in the same series while *E. esula* is in another series. Most of the Canadian leafy spurge seems to be referable to *E. virgata* or *E. × pseudovirgata* (McNiel, *in litt.* 1980). Thus *E. cyparissias* may be a better source of agents than *E. esula* s. str. Indeed, *E. esula* s. str. appears to lack aggressiveness and have a limited distribution in North America, so it may not warrant biological control. Of course the best source of agents are the target taxa themselves at their center of origin. The tetraploid cypress spurge is more aggressive than the diploid; but as they seem to be attacked by the same organisms, there is no need to distinguish between them for biological control purposes.

Species†	Host plants‡	Part damaged	Reference
MYXOMYCOTA§			
Myxomycetes			
Metatrichia horrida Ing	Euphorbia		47
EUMYCOTA			
MASTIGOMYCOTINA			
Oomycetes			
*Peronospora cyparissiae DeBary	2, E. amygdaloides	Foliage	70, 91
*Peronospora euphorbiae Fuckel	1, 3, 4	Foliage	70, 91
ASCOMYCOTINA			
Discomycetes			
Helotium cyparissias Velenovsky	2		
H. euphorbiae Velenovsky	2, polyphagous		94
Hypoderma commune (Fr.) Duby	2, polyphagous	Stems	94
H. virgultorum D.C.	Polyphagous		70
H. virgultorum	2	Stems	70
var. euphorbiae cyparissiae VC			
Lophodermium euphorbiae Velenovsky	2		94
Naevia tithymalina Rehm	2, E. gerardiana	Stems	70
Orbilia cyparissias Velenovsky	2		94
Phialea scutula Gill	2, polyphagous	Stems	70
Loculoascomycetes			
Guignardia rathenowiana Kirschst.	Euphorbia		52
*G. euphorbiae Akhundov	E. boisseriana		2
* <i>Leptosphaeria euphorbiae</i> Niessl	2		70
*L. euphorbiae var. Esulae Feltg.	1	Stems	70
L. tolgorensis Petrak	Euphorbia		73
Micropeltis euphorbiae Batista	Euphorbia		6
M. ugandae Hansford	Polyphagous		34
*Mycosphaerella cyparissincola Petrak	2		75
<i>M. parjumanica</i> Petrak	Euphorbia		74
Pleospora platyspora Sacc.	Polyphagous	Stems	70
Saccothecium hercynicum Kirschst.	2		1, 53
(= Pringsheimia)			
Schizothyrium snowdenii Hansford	Euphorbiaceae		34
Pyrenomycetes			
Eutypella euphorbiae Urries	Euphorbia		90
Gnomonia tetraspora Wint.	2	Stems	70
G. tithymalina Sacc. & Briard	2, E. palustris	Stems	70
Leptosphaeriopsis ophioboloides	1	Branches	70

Table 2. Fungi associated with *Euphorbia*.

(Sacc.) Berl. var. euphorbiae Feltg.			
*Leveillula lanata (Magn.) Golov.	Euphorbiaceae		10
Meliola ugandensis Hansford	Euphorbia		33
*Microsphaera euphorbiae (Petrak)	Euphorbia		91
Berk. & Curt. (M. coluteae Komarov)			
Nectria dacrymycella (Nyl.) Karst.	Polyphagous	Stems	70
*Oidium cyparissiae Syd.	2	Foliage, fruits	10, 70
(not Sphaerotheca euphorbiae)			
Physalospora minutula Sacc. & Speg.	2	Stems	70
Sphaerella cyparissiae Pass.	2	Stems	70
S. tithymali Pass.	2	Stems	70
Sphaerotheca tomentosa Otth	Euphorbia		10
(S. euphorbiae (Cast.) Salmon)			
BASIDIOMYCOTINA			
Hymenomycetes			
Dacryomyces euphorbiae Lasch	2	Stems	70
Typhula euphorbiae Fr.	2,4	Stems	70
(= Pistillaria euphorbiae Fuckel			
var. virescens Niessl)			
Teliomycetes			
Uredinales			
Uredinales * <i>Melampsora helioscopiae</i> (Pers.) Cast.	1, 2, 4	Leaves, stems	28
	1, 2, 4 1, 2, 3, 4	Leaves, stems Leaves, stems	28 4, 16, 28
*Melampsora helioscopiae (Pers.) Cast.			
* <i>Melampsora helioscopiae</i> (Pers.) Cast. * <i>M. euphorbiae</i> (Schub.) Cast.			
* <i>Melampsora helioscopiae</i> (Pers.) Cast. * <i>M. euphorbiae</i> (Schub.) Cast. (= <i>M. cyparissiae</i> W. Müller)	1, 2, 3, 4		4, 16, 28
 *Melampsora helioscopiae (Pers.) Cast. *M. euphorbiae (Schub.) Cast. (= M. cyparissiae W. Müller) *M. monticola Mains 	1, 2, 3, 4		4, 16, 28 4, 16, 28, 91
 *Melampsora helioscopiae (Pers.) Cast. *M. euphorbiae (Schub.) Cast. (= M. cyparissiae W. Müller) *M. monticola Mains *Endophyllum euphorbiae silvaticae 	1, 2, 3, 4		4, 16, 28 4, 16, 28, 91
 *Melampsora helioscopiae (Pers.) Cast. *M. euphorbiae (Schub.) Cast. (= M. cyparissiae W. Müller) *M. monticola Mains *Endophyllum euphorbiae silvaticae (DC) Wint. 	1, 2, 3, 4 1, 4 4		4, 16, 28 4, 16, 28, 91 28
 *Melampsora helioscopiae (Pers.) Cast. *M. euphorbiae (Schub.) Cast. (= M. cyparissiae W. Müller) *M. monticola Mains *Endophyllum euphorbiae silvaticae (DC) Wint. *E. euphorbiae nicaeensis Lion 	1, 2, 3, 4 1, 4 4 4	Leaves, stems	4, 16, 28 4, 16, 28, 91 28 28
 *Melampsora helioscopiae (Pers.) Cast. *M. euphorbiae (Schub.) Cast. (= M. cyparissiae W. Müller) *M. monticola Mains *Endophyllum euphorbiae silvaticae (DC) Wint. *E. euphorbiae nicaeensis Lion *Uromyces scutellatus (Pers.) Lév. 	1, 2, 3, 4 1, 4 4 1, 2, 3, 4	Leaves, stems Shoots	4, 16, 28 4, 16, 28, 91 28 28 4, 28
 *Melampsora helioscopiae (Pers.) Cast. *M. euphorbiae (Schub.) Cast. (= M. cyparissiae W. Müller) *M. monticola Mains *Endophyllum euphorbiae silvaticae (DC) Wint. *E. euphorbiae nicaeensis Lion *Uromyces scutellatus (Pers.) Lév. *U. kalmusii Sacc. 	1, 2, 3, 4 1, 4 4 1, 2, 3, 4 1, 2	Leaves, stems Shoots Shoots	4, 16, 28 4, 16, 28, 91 28 28 4, 28 28 28
 *Melampsora helioscopiae (Pers.) Cast. *M. euphorbiae (Schub.) Cast. (= M. cyparissiae W. Müller) *M. monticola Mains *Endophyllum euphorbiae silvaticae (DC) Wint. *E. euphorbiae nicaeensis Lion *Uromyces scutellatus (Pers.) Lév. *U. kalmusii Sacc. *U. alpestris Tranzschel 	1, 2, 3, 4 $1, 4$ 4 $1, 2, 3, 4$ $1, 2$ 2	Leaves, stems Shoots Shoots Flowers	4, 16, 28 4, 16, 28, 91 28 28 4, 28 28 28 28 28
 *Melampsora helioscopiae (Pers.) Cast. *M. euphorbiae (Schub.) Cast. (= M. cyparissiae W. Müller) *M. monticola Mains *Endophyllum euphorbiae silvaticae (DC) Wint. *E. euphorbiae nicaeensis Lion *Uromyces scutellatus (Pers.) Lév. *U. kalmusii Sacc. *U. alpestris Tranzschel *U. striolatus Tranzschel 	1, 2, 3, 4 1, 4 4 1, 2, 3, 4 1, 2 2 2	Leaves, stems Shoots Shoots Flowers Shoots	4, 16, 28 4, 16, 28, 91 28 28 4, 28 28 28 28 28 28 28
 *Melampsora helioscopiae (Pers.) Cast. *M. euphorbiae (Schub.) Cast. (= M. cyparissiae W. Müller) *M. monticola Mains *Endophyllum euphorbiae silvaticae (DC) Wint. *E. euphorbiae nicaeensis Lion *Uromyces scutellatus (Pers.) Lév. *U. kalmusii Sacc. *U. alpestris Tranzschel *U. striolatus Tranzschel *U. cristulatus Tranzschel 	1, 2, 3, 4 1, 4 4 1, 2, 3, 4 1, 2 2 2 4	Leaves, stems Shoots Shoots Flowers Shoots Shoots	4, 16, 28 4, 16, 28, 91 28 28 4, 28 28 28 28 28 28 28 28 28
 *Melampsora helioscopiae (Pers.) Cast. *M. euphorbiae (Schub.) Cast. (= M. cyparissiae W. Müller) *M. monticola Mains *Endophyllum euphorbiae silvaticae (DC) Wint. *E. euphorbiae nicaeensis Lion *Uromyces scutellatus (Pers.) Lév. *U. kalmusii Sacc. *U. alpestris Tranzschel *U. striolatus Tranzschel *U. cristulatus Tranzschel *U. tinctoriicola Magn. 	1, 2, 3, 4 1, 4 4 1, 2, 3, 4 1, 2 2 2 4 4	Leaves, stems Shoots Shoots Flowers Shoots Shoots	4, 16, 28 4, 16, 28, 91 28 28 4, 28 28 28 28 28 28 28 28 28 28 28 28 28
 *Melampsora helioscopiae (Pers.) Cast. *M. euphorbiae (Schub.) Cast. (= M. cyparissiae W. Müller) *M. monticola Mains *Endophyllum euphorbiae silvaticae (DC) Wint. *E. euphorbiae nicaeensis Lion *Uromyces scutellatus (Pers.) Lév. *U. kalmusii Sacc. *U. alpestris Tranzschel *U. striolatus Tranzschel *U. cristulatus Tranzschel *U. tinctoriicola Magn. *U. laevis Koern. 	1, 2, 3, 4 $1, 4$ 4 $1, 2, 3, 4$ $1, 2$ 2 2 4 4 4	Leaves, stems Shoots Shoots Shoots Shoots Shoots Shoots	4, 16, 28 4, 16, 28, 91 28 28 4, 28 28 28 28 28 28 28 28 28 28 28 28 28 2
 *Melampsora helioscopiae (Pers.) Cast. *M. euphorbiae (Schub.) Cast. (= M. cyparissiae W. Müller) *M. monticola Mains *Endophyllum euphorbiae silvaticae (DC) Wint. *E. euphorbiae nicaeensis Lion *Uromyces scutellatus (Pers.) Lév. *U. kalmusii Sacc. *U. alpestris Tranzschel *U. striolatus Tranzschel *U. tinctoriicola Magn. *U. laevis Koern. *U. sublevis Tranzschel 	1, 2, 3, 4 $1, 4$ 4 $1, 2, 3, 4$ $1, 2$ 2 2 4 4 4 4	Leaves, stems Shoots Shoots Shoots Shoots Shoots Shoots	4, 16, 28 4, 16, 28, 91 28 28 4, 28 28 28 28 28 28 28 28 28 28 28 28 28 2
 *Melampsora helioscopiae (Pers.) Cast. *M. euphorbiae (Schub.) Cast. (= M. cyparissiae W. Müller) *M. monticola Mains *Endophyllum euphorbiae silvaticae (DC) Wint. *E. euphorbiae nicaeensis Lion *Uromyces scutellatus (Pers.) Lév. *U. kalmusii Sacc. *U. alpestris Tranzschel *U. cristulatus Tranzschel *U. tinctoriicola Magn. *U. laevis Koern. *U. sublevis Tranzschel Uromyces anthyllidis (Grev.) Schroet. U. punctatus Schroet. U. jordianus Bubak. 	1, 2, 3, 4 1, 4 4 1, 2, 3, 4 1, 2 2 2 4 4 4 4 4 4 2/Anthyllis	Leaves, stems Shoots Shoots Shoots Shoots Shoots Shoots	4, 16, 28 4, 16, 28, 91 28 28 4, 28 28 28 28 28 28 28 28 28 28 28 28 28 2
 *Melampsora helioscopiae (Pers.) Cast. *M. euphorbiae (Schub.) Cast. (= M. cyparissiae W. Müller) *M. monticola Mains *Endophyllum euphorbiae silvaticae (DC) Wint. *E. euphorbiae nicaeensis Lion *Uromyces scutellatus (Pers.) Lév. *U. kalmusii Sacc. *U. alpestris Tranzschel *U. striolatus Tranzschel *U. tinctoriicola Magn. *U. laevis Koern. *U. sublevis Tranzschel U. sublevis Tranzschel U. sublevis Tranzschel 	1, 2, 3, 4 1, 4 4 1, 2, 3, 4 1, 2 2 2 4 4 4 4 4 2/Anthyllis 2, 3,/Astragalus, Oxytropis	Leaves, stems Shoots Shoots Shoots Shoots Shoots Shoots	4, 16, 28 4, 16, 28, 91 28 28 4, 28 28 28 28 28 28 28 28 28 28 28 28 28 2

<i>U. laburni</i> (DC) Fuckel.	2, 4,/Cytisus, Genista		4, 28
(U. cytisi (Strauss) Schroet.)			
(U. genistae Fuckel.)			
(U. genistae tinctoriae (Pers.) Wint.)	2/Lotus		1 29
<i>U. loti</i> Blytt <i>U. striatus</i> Schroet.		144	4, 28
U. onobrychidis (Desm.) Lév.	1, 2, 3, 4,/Medicago, Trifoliu. 2,/Onobrychis	m	4, 16, 28, 71 28
• • •	1, 2,/Lathyrus, Pisum		4, 28
U. pisi (Pers.) Wint. U. fischeri eduardi Magn.	1, 2, <i>Lainyrus</i> , <i>Fisum</i> 1, 2, 3,/Vicia		4, 28
U. dianthi (Pers.) Niessl	4,/ <i>Dianthus</i> ,		28
	Arenaria, Gypsophila		20
Teliomycetes			
Ustilaginales			
*Melanotaenium euphorbiae (Lenz)	3		54
Whit. et Thirumb.			
*Ustilago euphorbiae Mundkur	E. dracunculoides		99
*Tilletia euphorbiae Lenz	Euphorbia	Stems, peduncles	99
DEUTEROMYCOTINA			
Coelomycetes			
Asteroma euphorbiacearum Grove	E. amygdaloides		30
Diplodia euphorbiae Braunaud	E. teraculii	Dead stems	50
Haplosporella iranica Petrak	Euphorbia		74
Hendersonia euphorbiae Petrak	2		72
Leptostroma herbarum (Fr.) L.	Polyphagous	Stems	70
L. omissum Hilitzer	Polyphagous	Stems	42
L. punctiforme Wallr.	Polyphagous	Foliage	70
Leptostromella hysterioides Sacc.	Polyphagous	Stems	70
Leptothyrium capsicum Szambel	3, E. uralensis, E. gerardiana		88
Phoma cyclospora Sacc.	2, 4	Stems	70
*P. cyparissiae Guyot	2		31
*P. euphorbiicola (Schw.) Starb.	E. marginata		91
Phyllostictina euphorbiae Petrak	Euphorbia		74
Pseudodiplodia euphorbiarum Petrak	2		75
Septoria bractearum Mont.	Euphorbia	Branches	70
S. euphorbiae (Lasch) Desm.	1, 4, Euphorbia	Foliage	70
(= Ascochyta euphorbiae Lasch)			
<i>S. guepini</i> Oud. (= S. <i>euphorbiae</i> Guép.)	1,4	Foliage	45
Sphaeronaema euphorbiae Hollos	2		
Spaeropsis euphorbiae Pass.	Euphorbia	Stems	70
Vermicularia trichella Fr.	3	Stems	29
f. caulicola Gonz. Frag.			

Hyphomycetes			
Alternaria tenuis auct. sensu	Polyphagous		16, 91
Wiltshire			
Arthrinium euphorbiae M.B. Ellis	Euphorbia	Dead stems	25
Blastotrichum confervoides	Euphorbia	Stems	1, 70
Cda., nomen dubium			
*Cercospora euphorbiae	2, Euphorbia		99
Kell. & Swing			
*Fusicladium euphorbiae	3		51
Karakul.			
Phymatotrichum omnivorum	2, Euphorbia		91
(Shear) Dug.			
*Sclerotium cyparissiae DC	2	Foliage	91
S. euphoribiae-salicifoliae	E. salicifolia		82
Savul. & Sandu			
Stemphylium floridanum Hanon &	Euphorbia		66
Weber var. <i>euphorbiae</i> NagRaj &			
Govindu †Species with * are possible biocontrol agents.			
$\frac{1}{2}$ $E_{\rm contraction}$ $\frac{2}{2}$ $E_{\rm contraction}$			

[‡]1. *E. esula* 3. *E. virgata*

2. *E. cyparissias* 4. related *Euphorbia* species

§ classification after: Ainsworth, G.C. 1973. Introduction and keys to higher taxa, pages 1-7 in G.C. Ainsworth, F. K. Sparrow, and A.S. Sussman, eds., The Fungi, An Advanced Treatise, vol. IVA. A Taxonomic Review with keys: Ascomycetes and Fungi Imperfecti. Academic Press, New York, 621 pp.

VI. Progress toward the biological control of leafy spurge

The defoliating moth *Hyles euphorbiae* (L.) (Sphingidae) was released against the tetraploid form of *E. cyparissias* at Braeside, Ontario, in 1968 (37). The moth became established and spread over approximately 7770 ha that had patches of cypress spurge. The larvae reached a density of $1-2/m^2$ but as New (69) determined that at least 14 larvae/m² were necessary for defoliation, the weed is far from being controlled. However, in places in southern Ontario and New York State densities have reached 27-32 larvae/m² (7, 36). The moth was released on leafy spurge stands across Canada and at several sites in the United States and has become established in Montana (R. Nowierski, personal communication). The failure at other sites has been attributed to predation by ants and carabids.

In 1977 two Sesiid moths, *Chamaesphecia empiformis* Esp. and *C. tenthrediniformis* D. & S., were released against *E.* × *pseudovirgata* in Canada and against unspecified leafy spurge taxa in the United States, but they failed to become established (36). It was originally thought that *C. empiformis* attacked both *E. cyparissias* and *E. esula* but it was found that the host plants were not interchangeable; the moths had different life cycles and eggs of different size and color. The *E. esula* moth is now *C. tenthrediniformis* (67). No species of *Chamaesphecia* has been found on *E.* × *pseudovirgata* in Europe.

Feeding tests showed that the root-boring beetle *Oberea erythrocephala* (Schrank) developed on *E. cyparissias, E. esula, E. virgata* and *E. seguieriana* but not on other *Euphorbia* species or other plants tested (83). A release made in Saskatchewan in late 1979 has established but is increasing little. Larger releases were made in Canada and the United States in the summer of 1980. Good oviposition occurred at the three Canadian sites, but at one only 3% of the larvae had bored down the stems into the root before winter; at another 30% of the larvae were successful, and at the third site 69% were successful. Reasons for these differences are not known (36). At high rates of attack in Europe this beetle reduced the number of flowering spurge stems by 85% in the following year (83).

The root-feeding beetles *Aphthona flava* Guill. and *A. cyparissias* Koch were released on either leafy or cypress spurge in Alberta, Saskatchewan, Manitoba, Ontario, and Quebec. In Europe these beetles normally breed on spurges in the *E. esula-E. virgata* complex and in tests there was little or no development on other *Euphorbia* spp. (85). They occur together over much of western Europe, although *A. flava* has a slightly more southern distribution and may not be less cold hardy on the Canadian prairies (59). *A. cyparissias*, on the other hand, is equivalent in cold hardiness to flea beetles native to the prairies. In fact, both species completed a generation in Alberta and Saskatchewan in 1984. The effect of the larval damage to the roots is likely to be most pronounced on dry sites where the spurge is under water stress.

The leaf-tying moth *Lobesia euphorbiana*. Frr. was approved for release in 1982. In the laboratory normal development was restricted to some spurges of the subsections Chamaesyceae, Galarrhaei and Esulae. The larvae web the leaves of the terminal shoots together and the main effect of the attack is expected to be a decrease in seed production. Feeding tests on *L. occidentis* Falk. showed that newly hatched larvae did not accept Saskatchewan leafy spurge, so the insect is of no interest for biological control (Harris, unpublished data).

Attempts to establish a colony of the aphid *Acyrthosiphon neerlandicum* HRL in quarantine were unsuccessful as it would not breed on E. × *pseudovirgata*. *E. esula*, its host plant in Holland, was not available for the studies. This aphid warrants further investigation if a monophagous *E. esula* insect is required.

The tent caterpillar *Malacosoma castrensis* L. is found on leafy spurge in eastern Europe, although in Austria its normal host is *Sanguisorba* (Rosaceae). *M. castrensis* from leafy spurge developed on kohlrabi in feeding tests but on no other plant outside the genus *Euphorbia* including *Sanguisorba* and *Brassica* species (100). Possibly there are host races of this insect.

Feeding tests on the leaf-tying moth *Clepsis strigana* Hb. showed that it fed indiscriminately on a wide range of plants. Hence it is not suitable as a biocontrol agent.

Presently the following agents are being investigated:

1. A bud gall midge *Bayeria capitigena* Bremi. In the laboratory it bred on both *E. cyparissias* and *E.* × *pseudovirgata*.

2. A defoliating moth *Minoa murinata* Scop. In the laboratory it favored spurges in the subsections Galarrhaei and Esulae. Screening tests were completed in 1985 (Harris, unpublished data).

3. *Aphthona czwalinae* has a more eastern distribution in Europe, and it may be better suited for the wooded areas of Manitoba (59). It was approved for release in 1984.

4. Development of the lace bug *Oncochila simplex* H.-S. in feeding tests was restricted to certain *Euphorbia* species. The host records of thyme and tansy ragwort (19) were not confirmed by the tests.

5. Tests have started on a defoliating moth *Simyra dentinosa* Frey., which is common on leafy spurge in Greece and Turkey.

6. Studies have been started on the rust *Melampsora*, which is common on leafy spurge in western Europe, the Balkans and Asia.

7. The aphid, *Aphis esulae* CB, is damaging to North American leafy spurge under laboratory conditions and appear to be restricted to a few *Euphorbia* spp. It warrants further study.

Many of the candidate insect agents are attacked by specialized parasites and diseases that keep their populations low in Europe. Obviously if high densities of the agent are to be attained in North America, they should be released without these checks. The elimination of parasitic insects is no problem, but virus and microsporidian diseases are more difficult. It is usually necessary to rear the insects individually for several generations. So far the following diseases have been encountered. The stock of *Hyles euphorbiae* larvae imported from Europe contained both a cytoplasmic and a nuclear virus. Sommer and Maw (85) reported that many species of beetles in the genus *Aphthona* were infected with *Nosema* that caused high larval mortality and a disease has been reported in *Simyra dentinosa* (Campobasso *in litt.* 1980).

VII. Conclusions

Application of herbicides is difficult and expensive on rough terrain; thus, for large infestations of leafy spurge on marginal land chemical control is not economic. As a result leafy spurge continues to spread and dominate large areas of marginal agricultural land in North America. The prospects are excellent that biological control can reduce the aggressiveness of the weed on these sites by establishing spurge insects and pathogens from Europe and Asia.

The conflicts of interest associated with the biological control of leafy spurge can be minimized by using narrowly specialized agents. Fortunately there is a good selection of species, some of which are restricted to a single taxon of the weed. Reduction of the weed to below the economic threshold is likely to require the establishment of four agents on each taxon of the weed. Hopefully it will be possible to reduce the total number of agents required by using species that attack several taxa and still not threaten desirable spurges. Unless this can be done control of E. × *pseudovirgata* may be difficult since hybrids sometimes escape attack from the specialized enemies of both parents. This has occurred with the hybrid prickly pear, *Opuntia aurantiaca* (3).

Considerable progress has been made in determining the agent resource available for biological control, and studies to determine host ranges are proceeding. The moth *H. euphorbiae* has been established in North America and the beetle *O. erythrocephala* appears likely to become established. The moths *C. empiformis* and *C. tenthrediniformis* can probably be established if they are released on the correct spurge taxon.

The urgent need is to determine the distribution, aggressiveness and ecology of the various taxa of leafy spurge in North America. The absence of this basic knowledge has been the main reason that more progress has not been made on the biological control of leafy spurge.

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