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Native plant considerations in the biological control of leafy spurge[1]

R. W. PEMBERTON

The author works for the United States Department of Agriculture, Agricultural Research Service, Biological Control of Weeds Research Unit, Albany, CA 94706, U.S.A.

Abstract:

In North America leafy spurge is a complex of forms, species, and hybrids which has most frequently been called *Euphorbia esula*. Leafy spurge is a deep-rooted perennial weed that is primarily a problem in the Great Plains region of the U.S. and Canada because it is toxic to some classes of livestock and displaces more desirable forage plants. Biological control research, which was begun in the early 1960s, has yet to produce insects which cause a reduction in the plants, but still holds promise. A significant consideration with the biological control effort on leafy spurge is the presence of 107 native *Euphorbia* and four or five native *Chamaesyce* species which could be used and damaged by the agents introduced for leafy spurge control. Almost one-third of these native spurges are sympatric with leafy spurge. Although these natives have no known economic value, 11 are rare and under review for Federal protection as threatened or endangered species. Even though *Euphorbia purpurea*, in the mideastern U.S. is the only rare species under review which is sympatric with leafy spurges, other rare spurges could also be attacked. This is based on the large number (25) of spurges that are sympatric with both leafy spurge and the rare spurges which could serve as bridges to carry the biological agents from leafy spurge to the rare species. Just what the actual levels of risks are, or what damage to or even elimination of some native spurges would mean are complex issues, relating not only to the scientific possibilities and effects, but also to the various interests and values of our country. To what extent the use of native spurges would occur depends primarily upon the host plant specificity levels (within the genus *Euphorbia*) of the agents involved since most of the insects have relatively broad climatic tolerances. There are large differences in the host plant specificity levels of the leafy spurge insects, although not much is known about this for the insects

[1] E. S. Delfosse, editor.

utilized earlier in the program (*Hyles euphorbia* and *oberea erythrocephala*). The current strategy is to select among the newer candidates, and the other as yet unknown organisms, species which are broad enough in their host ranges to accept the diverse forms of leafy spurge and yet narrow enough to exclude the use of most native spurges, and the rare species under review in particular. While the leaf-tier, *Lobesia Euphorbiana*, seems likely to be able to use most native spurges, it appears that *Aphthona flava,* a root-borer, and *Bayeria capitigena*, a shoot gall midge, with host plant specificity levels below the subgenus Esula level, do meet these criteria. These two insects may help us to begin to reduce the abundance of leafy spurge while remaining attentive to the native spurge considerations.

Introduction

In North America, leafy spurge is a complex of forms, species, and hybrids which has most frequently been called *Euphorbia esula* L. (Euphorbiaceae). The most common problem type appears to be *E.* × *pseudovirgata* which is a hybrid of *E. esula sensu stricto* and *E. waldsteinii* (= *E. virgata* Waldst. & Kit.) (Dunn and Radcliffe-Smith 1980). *E. esula's* range in its native Eurasia is from Spain and Portugal (Radcliffe-Smith and Tutin 1968) to China (Steward 1958) and Japan (Ohwi 1965). *E. waldsteinii* (as *E. virgata*) is native to central and eastern Europe (Radcliffe-Smith and Tutin 1968). The taxonomy of this leafy spurge complex is not yet resolved and is under study by a number of workers.

Leafy spurge (Fig. 1) is a perennial herb with a deep and extensive root system. The plants reproduce vegetatively to form persistent patches which coalesce to form large stands. Spread is by seed, which can be ejected as far as 5 miles from their explosive capsules (Bakke 1936). Animals, water, and human activities are thought to serve to disperse the seed (Selleck *et al*. 1962). This spurge has very broad ecological tolerances (Selleck *et al*. 1962).

Leafy spurge was first recorded in the U.S. at Newburry, Massachusetts, in 1827 (Britton 1921) but probably has had many separate introductions (Dunn 1979). Its distribution in the U.S. (as of 1979) is shown in

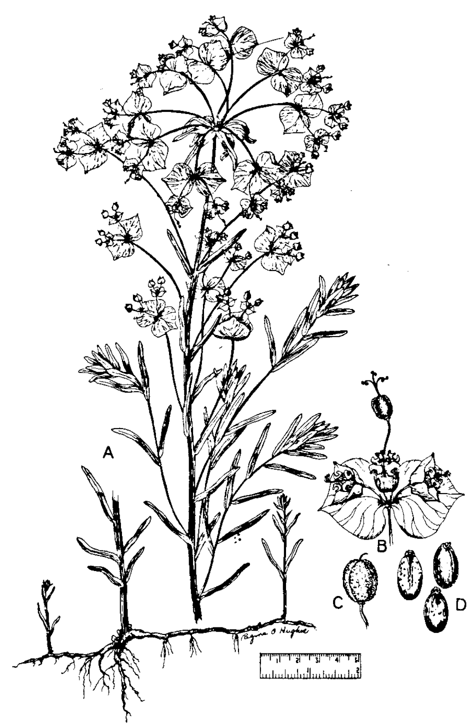

Fig. 1. Leafy spurge (*Euphorbia esula* L. complex (after Reed and Hughes 1970).

Fig. 2 (Dunn 1979). The main problems caused by leafy spurge are toxicity to some classes of livestock, and reduction of desirable forage plants, which occurs through competition (Selleck 1959) and selective grazing by cattle which usually refuse to eat the plant (Dunn 1979). Peter Harris' (Agric. Can., Regina, Saskatchewan, pers. comm.) examination of the change in the spurge abundance over a 30-yr period in Saskatchewan found that the plant "disappeared in the course of normal agricultural practices on land broken for cereal production but on permanent grasslands the infested area had approximately doubled in spite of the control program". The primary control method used against leafy spurge has been with selected herbicides.

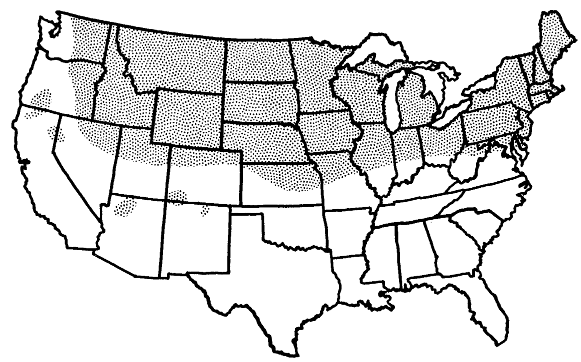

Fig. 2. The distribution of leafy spurge in the United States as of 1979 (modified from Dunn 1979).

A biological control program against this weed was initiated in the early 1960s by Canada in response to its spread and the high costs of chemical control. The first leafy spurge biological control agent, the leafy spurge hawk moth, *Hyles euphorbiae* (Lepidoptera: Sphingidae), was imported from Europe and released in North America beginning in 1965 (Harris 1984). The U.S. Department of Agriculture joined the effort in the mid-1970s, at first only to utilize insects cleared for introduction by the Canadians, then to develop its own candidate agents. After > 20 years since the program was initiated, a number of insect species have been released against leafy spurge (discussed later), but not much progress had been made. Although a large number of insects are restricted to the genus in Europe, it has been difficult to find species which will survive and be effective in North America on a leafy spurge which seems to be a complex (Harris 1984). It is probable that a complex of biological control agents exerting an intense level of pressure on the plants will be required for leafy spurge to be reduced, since plants can readily regenerate from their latex-rich root system following destruction of the above-ground stems. When leafy spurge is managed using sheep, the animals need to be continuously pastured with the plants to keep the latter's density low. These factors suggest that even before (or without) the native spurge conflict, that biological control of leafy spurge has been, and is, a difficult task.

An examination of the native plant issue with the biological control of leafy spurge program was begun for a number of reasons. First was the recognition of the large number of U.S. native spurges (*Euphorbia* and *Chamaesyce* species) that could become non-target hosts for biological control agents introduced against leafy spurge. Secondly, U.S. environmental legislation was passed which regulated the action of the Federal Government agencies in relation to the environment (the National Environmental Policy Act, NEPA, 1969, U.S. Government Council on Environmental Quality, 1978; and the Endangered Species Act, 1973, 1978). Part of the Endangered Species Act was the listing, by the U.S. Fish and Wildlife Service (1980, 1983), of many rare spurges as candidates for legal protection as endangered or threatened species. Finally, detection of movement of insects introduced for biological control of weeds, from the target weeds to their non-target native relatives, in four of the USDA's past projects: from *Silybum marianum* (L.) Gaertn. and *Carduus* spp. to *Cirsium* spp. (all Asteraceae) (Turner, Pemberton, and Rosenthal, unpubl. data); from *Tribulus terrestris* L. to *Kallstroemia* spp. (both Zygophyllaceae) (Hawkes and Turner, unpubl. data); from *Hypericum perforatum* L. to *Hypericum* spp. (Clusiaceae) (Andres 1985); and from *Alternanthera philoxeroides* (Mart.) Griseb. to *Philoxerus vermicularis* (L.) R. Br. ex J.E. Smith (both Amaranthaceae) (Vogt, USDA, Stoneville, Miss., unpubl. data). Although the effects of these movements are unknown, they are not necessarily significant. However when coupled with the above-mentioned legislation plus the large numbers of native spurges that occur in North America, an analysis of the potential use of these plants by candidate agents seemed necessary.

To understand the nature of the biological control of leafy spurge-native plant issue, I examined the numerous plant species, their diverse taxonomic affinities, geographic distributions, and other characteristics which relate to their potential use by biological control agents. The native spurges which are used in the host plant specificity testing are then discussed. This will be followed by a description of the principal leafy spurge insects, their known host plant specificity levels, and current status in the project. After this, a discussion of the potential risks of use and harm to native spurges, and the meaning and implications of this use will be made. In conclusion are some comments on the strategy and prognosis in dealing with this leafy spurge-native spurge issue.

The Plants

Table 1 lists the spurges which occur in America north of Mexico. There are 111- 112 native spurges (107 *Euphorbia* spp. and 4-5 native *Chamaesyce* spp.) and 13 introduced *Euphorbia* spp. *Chamaesyce* and *Euphorbia* are closely related genera in the Euphorbiaceae. The subgenus *Chamaesyce*, within the genus *Euphorbia*, frequently has had many or all of its species placed in the genus *Chamaesyce* and vice versa. Insects which have 'genus' level host specificity breadths usually feed on both *Chamaesyce* and *Euphorbia* spp. The subgenus for each of the spurge species is listed in Table 1. The subgeneric concept is not only a very useful way of dealing with the large number of *Euphorbia* spp., but also appears to provide quite 'natural' groupings which reflect true phylogenies (M. Huft, Field Museum, Chicago, pers. comm.). Many *Euphorbia*-feeding insects respond to these subgenera, accepting as host plants most of the species in one or more of the subgenera and rejecting the species in other subgenera.

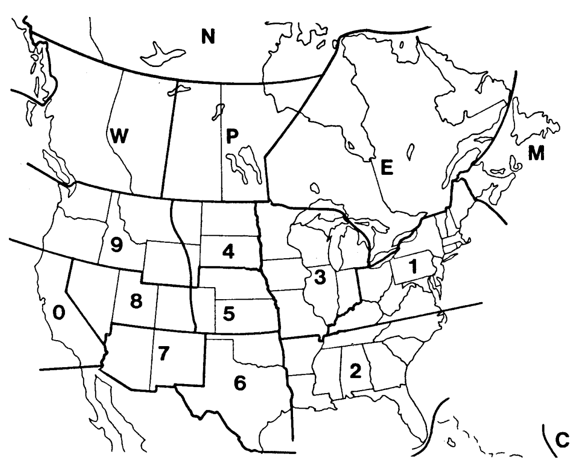

Fig. 3. Regional distribution codes for the spurge species listed in Table 1 (from U.S. Department of Agriculture 1982).

In North America, there are four subgenera including Esula with 21 spp., Agaloma with 26 spp., Poinsettia with 3 spp., and Chamaesyce with 57 spp. (This information and much of that relating to the characteristics of spurges was compiled from the references listed in the literature cited section and marked with an asterisk.) In Europe all but 4 of the 105 *Euphorbia* spp., which are subgenus Chamaesyce spp., belong to the subgenus Esula (Radcliffe-Smith and Tutin 1968). Leafy spurge belongs to the subgenus Esula. North American euphorbias which belong to this subgenus are then the most closely related species to leafy spurge and thus presumably the most subject (by taxonomic affinity) to use by agents introduced for leafy spurge control. All of the European host plant records for *Euphorbia*-feeding insects are from subgenus Esula spp. and therefore provide no indication whether North American Poinsettia, Agaloma or Chamaesyce spurges could become hosts for these insects.

Table 1 also provides distribution codes for each spurge species. Each code represents the occurrence of the plant in a particular region, as shown on the accompanying Soil Conservation Service map (Fig. 3). The next column in Table 1 indicates whether a particular spurge is sympatric with leafy spurge. These are the plant species that, depending on the level of host plant specificity for a particular agent, would be most likely to become host plants for leafy spurge biological control agents. In all, 32 and possibly as many as 41 native spurges have overlapping ranges with leafy spurge. Table 2 summarizes the numbers of spurges, their subgenera, habits, sympatric species with leafy spurge, rare review species, etc.

Table 1 also indicates whether a particular spurge is a rare species under review for Federal protection as a threatened or endangered species. Table 3 treats these rare review species a little more fully, giving more specific information about life form, habitat, location, and review category. Currently there are nine *Euphorbia* and two *Chamaesyce* spp. under review. Fig. 4 indicates the approximate location of these species. Most of these rare spurges are habitat specialists. Only one of these species, *E. purpurea* (Raf.) Ferald, which occurs in the mideastern U.S. is sympatric with leafy spurge. This species is a robust perennial which belongs to the subgenus Esula, qualities that could increase the risk of its use by spurge-feeding insects.

The possibility that other rare and endangered *Euphorbia* and *Chamaesyce* spp. could be used by insects introduced for leafy spurge control is still significant, even though there is no overlap in the distributions of these plants and leafy spurge. This is based on the large number of other spurge species which could serve as bridges to carry biological control agents from leafy spurge to the endangered spurges. For a spurge species to be a bridge, it must be first an acceptable host to a particular natural enemy, and then be sympatric with both leafy spurge and an endangered spurge. Table 1 identifies at least 25 spurge species which could become bridges. It is also possible, but more difficult, for natural enemies to move from leafy spurge to a species under review through a series of other spurge species, which individually could not bridge the total distance between them.

Table 1. *Euphorbia* and *Chamaesyce* species which occur in America North of Mexico[1].

Euphorbia or *Chamaesyce* species (* introduced species, others are native)	Habit	Subgenus (and sections for esulas)	Distribution codes[2]	Sympatric with leafy spurge	Rare species under review for legal protec-tion	Potential bridge leafy spurge to a species under review
E. abramsiana L.C. Wheeler	Annual	chamaesyce	7 0			
E. acuta Engelm.	Perenn.	agaloma	6 7			
E. albomarginata Torr. & Gray	P	chamaesyce	6 7 8 0	possibly		possibly
E. alta J.B.S. Norton	P	esula sec. galarrhoei	7			
E. ammannioides H.B.K.	A	chamaesyce	1 2 6			
E. angusta Engelm.	P	agaloma	6			
E. antisyphilitica Zuccar	P	agaloma	6			
E. arizonica Engelm.	P	chamaesyce	6 7 0			
E. astyla Engelm. ex Boiss.	P	chamaesyce	6			
E. bicolor Engelm. & Gray	A	agaloma	2 6			
E. bifurcata Engelm.	A	agaloma	6 7			
E. bilobata Engelm.	A	agaloma	6 7			
E. blodgettii Engelm. A. Hitchc.	P	chamaesyce	2 0			
E. brachycera Engelm.	P	esula sec. esula	6 7 8	possibly		possibly
E. capitellata Engelm.	P	chamaesyce	7			
E. carunculata Waterfall	A	chamaesyce	6			
E. chamaesula Boiss.	P	esula sec. esula	7			
E. cinerascens Engelm.	P	chamaesyce	6			
E. commutata Engelm.	A	esula sec. esula	1 2 3 5 6 7	possibly		yes
E. conferta (Small) B.E. Smith	A	chamaesyce	2			
E. cordifolia Elliot	A	chamaescye	2 6			
E. corollata L.	P	agaloma	1 2 3 4 5 6 E	yes		yes
E. crenulata Engelm.	A	esula sec. esula	8 9 0	yes		yes
E. curtisii Engelm.	shrub	agaloma	2			
E. cyathophora Murray	A	poinsettia	1 2 3 4 5 6	yes		yes
**E. cyparissias* L.	P	esula sec. esula	1 2 3 4 5 8 9 H W P E M	yes		yes
E. deltoidea Engelm. ex Chapm.	P	chamaesyce	2		yes	
E. dentata Michx.	A	poinsettia	1 2 3 4 5 6 7 H E	yes		yes
E. discoidalis Chapm.	P	agaloma	2			
E. eriantha Benth.	A	agaloma	6 7 0			
**E. esula* L.	P	esula sec. esula	1 3 4 5 8 9 0 W P E M			
**E. exigua* L.	A	esula see. esula	1 6 0 W E M	yes		
E. exserta (Small) Coker	P	agaloma	2			
E. exstipulata Engelm.	A	agaloma	6 7			
**E. falcata* L.	A	esula sec. esula	1	yes		
E. fendleri Torr. & Gray	P	chamaesyce	4 5 6 7 8 9 0	yes	yes[3]	yes
E. flofida Engelm.	A	chamaesyce	7			

Euphorbia or *Chamaesyce* species (* introduced species, others are native)	Habit	Subgenus (and sections for esulas)	Distribution codes[2]	Sympatric with leafy spurge	Rare species under review for legal protection	Potential bridge leafy spurge to a species under review
E. flofidana Chapm.	P	esula sec. ipecacuanhe	2			
E. garberi Engelm. ex Chapm.	A	chamaesyce	2		yes	
E. geyeri Engelm.	A	chamaesyce	3 4 5 6 7 P	yes		yes
E. glyptosperma Engelm.	A	chamaesyce	1 3 4 5 6 7 8 9 0	yes		yes
E. golondrina L.W. Wheeler	A	chamaesyce	6		yes	
E. gracillima S. Wats.	A	chamaesyce	7			
**E. helioscopia* L.	A	esula sec. galarrhoei	1 2 3 6 9 0 W P E M	yes		
E. helleri Millsp.	A	esula sec. esula	6			
E. heterophylla L.	A	poinsettia	1 2 3 4 6 7	yes		yes
E. hexagona Nutt. ex Spreng.	A	agaloma	2 3 4 5 6	yes		yes
E. hirta L.	A	chamaesyce	2 6 7			
E. hooveri L.C. Wheeler	A	chamaesyce	0		yes	
E. humistrata Engelm.	A	chamaesyce	1 2 3 5 6	yes		yes
E. hyperifolia L.	A	chamaesyce	2 6			
E. hyssopifolia L.	A	chamaesyce	2 6 7			
E. incisa Engelm.	P	esula sec. esula	7 8 0	possibly		
E. indivia (Engelm.) Tidest.	A	chamaesyce	6 7			
E. innocua L.C. Wheeler	P	agaloma	6			
E. inundata Turr. ex Chapm.	P	esula sec. ipecacuanhe	2			
E. ipecacuanhae L.	P	agaloma	1 2	yes		possibly
E. jejuna A Johst. & Warnock.	P	chamaesyce	6			
E. laredana Millsp.	P	chamaesyce	6			
E. lata Engelm.	P	chamaesyce	5 6 7	yes		possibly
**E. lathryis* L.	A	esula sec. esula	1 2 7 9 0 W E	yes		
E. longicruris Scheele	A	esula sec. esula	2 6			
**E. lucida* Waidst. & Kit.	A	esula sec. esula	1 3 W P E	yes		
E. lurida Engelm.	P	esula sec. esula	7 8	yes		
E. macropus (Klotzsch & Garcke) Boiss.	P	agaloma	7			
E. maculata L. (= *E. supina*)	A	chamaesyce	1 2 3 4 5 6 7 9 0 E M	yes		yes
E. marginata Pursh	A	agaloma	1 2 3 4 5 6 P E	yes		yes
E. melanadenia Torr.	P	chamaesyce	7 0			
**E. mendezii* Boiss.	P	chamaesyce	2			
E. mercurialina Michx.	P	agaloma	1 2	yes		
E. mesembriantemifolia Jacq.	shrub	chamaesyce	2			
E. micromera Boiss.	A	chamaesyce	6 7 8 0	possibly		possibly
E. misera Benth.	shrub	agaloma	0			
E. missurica Raf.	A	chamaesyce	2 3 5 6 7 9	yes		yes
E. nephradenia Barneby	A	agaloma	8	yes		
**E. nutans* Lab.	A	chamaesyce	1 2 3 4 5 6 9 0	yes		yes

Euphorbia or *Chamaesyce* species (* introduced species, others are native)	Habit	Subgenus (and sections for esulas)	Distribution codes[2]	Sympatric with leafy spurge	Rare species under review for legal protec-tion	Potential bridge leafy spurge to a species under review
**E. oblongata* Griseb.	A	esula sec. esula	0			
E. obtusata Pursh	A	esula sec. galarrhoei	1 2 3 5 6	yes		yes
E. ocellata E.M. Durand & Hilgard	A	chamaesyce	7 8 0	yes		possibly
E. ophthalmica Pers.	A	chamaesyce	2			
E. palmari Engelm.	P	esula sec. esula	7 8 0	possibly		possibly
E. parishii Greene	P	chamaesyce	8 0			
E. parryi Engelm.	A	chamaesyce	6 7 8 0	yes		possibly
E. pediculifera Engelm.	P	chamaesyce	7 0			
E. piplidion Engelm.	A	esula sec. esula	6			
**E. peplus* L.	A	esula sec. esula	1 2 3 7 9 0 H W P E M	yes		yes
E. parennans (Shinners) Warnock & M. Johnst.	P	chamaesyce	6		yes	
E. pergamena Small	P	chamaescye	2			
**E. platyphylla* L.	A	esula sec. galarrhoei	1 3 E	yes		
E. platysperma Englem.	A	chamaesyce	0		yes	
E. polycarpa Benth.	P	chamaesyce	7 8 0	possibly		possibly
E. polyonifolia L.	A	chamaesyce	1 2 3 E M	yes		
E. polyphylla Engelm. ex Chapm.	P	agaloma	2			
E. prostrata Ait.	A	chamaesyce	2 5 6 7 0	yes		yes
E. pubentissima Michx.	P	agaloma	1 2	possibly		
E. purpurea (Raf.) Fernald	P	esula section[4]	1 2	yes	yes	
E. pychanthema Englem.	AP	chamaescye	6			
E. radicans Benth.	P	agaloma	6 7			
E. revoluta Englem.	A	chamaesyce	5 6 7 0			
E. robusta (Engelm.) Small	P	esula sec. esula	4 5 7 8 9	yes		yes
E. roemerana Scheele	A	esula sec. esula	6			
**E. segetalis* L.	A	esula sec. esula	1			
E. serpens H.B.K.	A	chamaesyce	1 2 3 4 5 6 7 8 9 0 E	yes		yes
E. serphyllifolia Pers.	A	chamaesyce	3 4 5 6 7 8 9 0 W P E M	yes		yes
E. serrula Englem.	A	chamaesyce	6 7	possibly		possibly
E. setiloba Engelm.	A	chamaesyce	6 7 8 0	possibly		possibly
E. simulans (L.C. Wheeler) Warnock & M. Johnst.	AP	chamaesyce	6			
E. spatulata Lam.	A	esula sec. galarrhoei	2 3 4 5 6 7 8 9 0	yes		yes
E. strictospora Engelm.	A	chamaesyce	3 4 5 6 7	yes		yes
E. strictior Holz	P	agaloma	6 7	possibly		
E. telephiodes Chapm.	P	esula sec. ipecacuanhe	2		yes	
E. tetrapora Engelm.	A	esula sec. esula	2 6			

Euphorbia or *Chamaesyce* species (* introduced species, others are native)	Habit	Subgenus (and sections for esulas)	Distribution codes[2]	Sympatric with leafy spurge	Rare species under review for legal protec-tion	Potential bridge leafy spurge to a species under review
E. theriaca L.C. Wheeler	A	chamaesyce	6			
E. trachysperma Engelm.	A	chamaesyce	7			
E. trichotoma H.B.K.	P	esula sec. esula	2			
E. vallis-mortae(Millsp.) J.T. Howell	P	chamaesyce	0			
E. vermiculata Raf.	A	chamaesyce	1 3 5 7 W E M	yes		
E. vilifera Scheele	P	chamaesyce	6			
E. wrightii Torr. & Gray	P	agaloma	6			
E. zinniiflora Small	P	agaloma	1 2	yes		
C. cumulicola Raf.	A	—	2		yes	
C. pinetorum Small	P	—	2			
C. porterana Small	P	—	2		yes	
C. serpens[5] (H.B.K.) Small	A	—	2			
C. thymifolia (L.) Millsp.	A	—	2			

[1] Based upon "National list of scientific plant names", Soil Conservation Service, authored by M. Huft. Field Museum of Natural History, Chicago.

[2]See the Soil Conservation Service map (Fig. 3) for the location of the distribution codes.

[3]Only *Europhorbia fendleri* : var. triligulata is under review, other subspecific taxa of *E. fendleri* are not being reviewed.

[4]*E. purpurea* not placed in a section by Norton (1900).

[5]Area of origin uncertain.

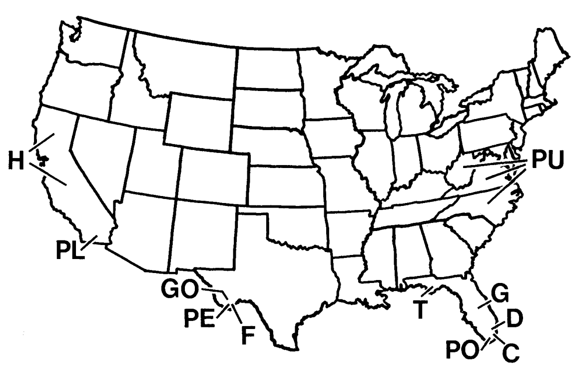

Fig. 4. Distribution of rare spurges which are under review for legal protection as threatened or endangered status. H = *Euphorbia hooveri* L.C. Wheeler, PL = *E. playsperma* Engelm., PE = *E. perennans* (Shinners) Warnock & M. Johnst., GO = *E. golondrina* L.W. Wheeler, F = *E. fenderli* Torr. & Gray var. *triligulata*, T = *E. telephiodes* Chapm., PU = *E. purpurea* (Raf.) Fernald, G = *E. garberi* Engelm. ex Chapm., D = *E. deltoidea* Engelm. ex Chapm., C = *Chamaesyce cumulicola* Raf., PO = *C. porterana* Small.

To what extent this bridging would occur depends primarily upon the host plant ranges of the biological control agents used. Leafy spurge's natural enemies, which have genus-level host specificity levels, could in theory use all 25 spurge bridges to move onto the 11 rare species under review. Agents which are restricted to using species of the subgenus Esula (the leafy spurge group) would have four potential bridges to *Euphorbia telephiodes* Chapm. This spurge is one of two subgenus Esula spp. under review, *E. purpurea* which is sympatric with leafy spurge is the other. Fig. 5 shows the distribution of *E. spatulata* Lam., a widespread subgenus Esula species which is a potential bridge. Figs. 6 and 7 show, respectively, the ranges of *E. maculata* L., a subgenus Chamaesyce potential bridge, and *E. marginata* Pursh, a subgenus Agaloma potential bridge. When these maps are compared with the map of leafy spurge (Fig. 2) and the map showing the occurrence of the spurges under review (Fig. 4), the potential for bridging can be seen.

The degree of use of native non-target spurges by leafy spurge biological control agents should be directly related to the breadth of their host ranges, which at this point is imperfectly known.

Table 2. North American spurges (*Euphorbia* and *Chamaesyce* summary list.

Euphorbia	
1. Number of *Euphorbia* species	
2. Number of introduced *Euphorbia* species	120
3. Number of native *Euphorbia* species (50 perennials and 57 annuals)	13
4. Number of native *Euphorbia* species in the subgenus esula	107
(12 perennials and 9 annuals)	21
5. Number of native *Euphorbia* species in the subgenus agaloma (14 perennials and 8 annuals)	26
6. Number of native *Euphorbia* species in the subgenus poinsettia (all perennials)	3
7. Number of native *Euphorbia* species in the subgenus chamaesyce (21 perennials and 36 annuals)	57
8. Number of native *Euphorbia* species sympatric with leafy spurge (7 esulas, 7 agalomas, 3 poinsettias and 15 chamaesyce) (9 other species may be sympatric with leafy spurge)	32
9. Number of rare *Euphorbia* species under review for legal protection as endangered or threatened species (variety triligulata of *E. fendleri* under review is included, other subtaxa of this species are not rare)	9
10. Number of potential species bridges that could carry introduced biological control agents from leafy spurge to rare *Euphorbia* species under review (7 esulas, 4 agalomas, 3 poinsettias and 11 Chamaesyce) (11 additional species may be potential bridges)	25
Chamaesyce	
1. Number of *Chamaesyce* species (2 perennials and 3 annuals)	5
2. Number of native *Chamaesyce* species (the origin of *E. mendezii* is uncertain)	4-5
3. Number of *Chamaesyce* species which are sympatric with leafy spurge or which could serve as bridges to rare species	0
4. Number of rare *Chamaesyce* species under review for endangered or threatened status	2
Totals	
Combined total of native spurge species (*Euphorbia* and *Chamaesyce*) in America north of Mexico	111-112
Total number of rare spurges under review for legal protection	11

Table 3. Rare spurges under review for legal protection as endangered or threatened species[1].

Species	Subgenus	Habit and Size	Habitat	Locality	Review Catagory[2]	Comments
1. *Chamaesyce cumulicola* Raf. (=*Euphorbia cumulicola*)	Chamaesyce of Euphorbia	prostrate or decumbent annual herb	Coastal dunes and scrub	Cape Romano region and lower southeastern coast of So. Fla.	2	
2. *C. porterana* Small (=*Euphorbia porterana*)	Chamaesyce of Euphorbia	erect or ascending perennial herbs 3-10 cm tall	Pinelands and coast scrub	Dade and Monroe Co. and the Keys of So. Fla.	1	probably will be proposed[3]
C.p. var. *keyensis*	"	"	Coastal scrub on limestone soils and sandy areas	Florida Keys	1	"
C.p. var. *porterana*	"	"	Pinelands on limestone soils	Dade & Monroe Co., Fla.	1	"
C.p. var. *scaparia*	"	"	Pinelands on limestone soils	lower Fla. Keys	1	"
3. *Europhorbia deltoidea* Engelm. ex Chapm.	Chamaesyce	prostrate perennial herbs forming dense mats	Pinelands	Dade Co. and Keys of Fla.	1	probably will be proposed[4]
E.d. spp. *deltoidea*	"	"	"	Dade Co. Fla.	1	"
E.d. spp. *serpyllum*	"	"	"	Lower Fla. Keys	1	"
4. *E. fenderli* Torr. & Gray var. *triligulata*	Chamaesyce	decumbent to erect perennial herb 5-15 cm long	—	Big Bend area of Texas	2	other subtaxa of *E. fenderli* are not rare

Table 3. Continued.

Species	Subgenus	Habit and Size	Habitat	Locality	Review Catagory[2]	Comments
5. *E. garberi* Engelm. ex Chapm.	Chamaesyce	robust prostrate or low ascending robusta annual herb to 3 cm long.	Pinelands and hamocks	Florida	1	
6. *E. golondrina* L.W. Wheeler	Chamaesyce	prostrate annual herb 5-35 cm long	Alluvial or eolian soils	Deserts of So. Brewster Co., Tex.	2	
7. *E. hooveri* L.C. Wheeler	Chamaesyce	prostrate or decumbent annual herb 5-20 cm long	Dried mud flats and dried vernal pools in Valley Grassland Community	Near Vina in Tehama Co. and Visalia in Tulare Co., Calif.	1	probably will be proposed[5]
8. *E. pevennans* (Shinners) Warnock & M. Johnst.	Chamaesyce	perennial herb 13-47 cm tall with 5-20 erect stems and woody tap root	Gypsum soils	Terlingua-Lajitas areas of S.W. Brewster Co., Texas	2	
9. *E. platysperma* Engelm.	Chamaesyce	prostrate annual 1-2.5 cm long	Sandy soil in in the Creosote Bush Community	Near Thousand Palms in Coachella Valley, Calif. and the Yuma area of Calif. and Ariz.	2	

Table 3. Continued.

Species	Subgenus	Habit and Size	Habitat	Locality	Review Catagory[2]	Comments
10. E. purpurea (Raf.) Fernald	Esula	perennial herb to 1 m tall growing from a short stout woody rhizome	Dry but more frequently moist or swampy woods and thickets	Carroll Co, Maryl.; Ashe, Buncombe, Haywood, Jackson, Macon, Mitchell and Watauga Co, N.C.; Rockbridge Co, Vir.; Pocahontas, Preston, Randolph and Tucker Co., W. Vir.	2 2	No action planned at present[6]
11. *E. telephiodes* Chapm.	Esula	robust perennial herb to .3 m	Dry sandy pine palmetto savannas	Near the Apalachicola river in Franklin Co. and Port St. Joe in Gulf Co. of panhandle, Fla.	2	Abundant within its very limited habitat[7]

[1]Based upon the 1980 U.S. Fish and Wildlife listing which was amended in 1983.

[2]Review categories for listed taxa were defined and assigned in the 1980 and 1983 listings. Catagory 1 indicates that sufficient information is on hand to support the biological appropriateness for the listing of a species to be listed as Endangered or Threatened.

[3]Andy Robinson, Botanist, Office of Endangered Species (FWS), Reg. 1, Portland, Oregon.

[4]Marshal Jones, Biologist, Office of Endangered Species (FWS), Reg. 4, Atlanta, Georgia.

[5]Jim Bartel, Botanist, Office of Endangered Species (FWS), Reg. 1, Sacramento, California.

[6]Dick Dyer, Botanist, Office of Endangered Species (FWS), Reg. 5, Newton Corner, Massachusetts.

[7]Marshal Johnston, Botanist, Department of Botany, University of Texas, Austin.

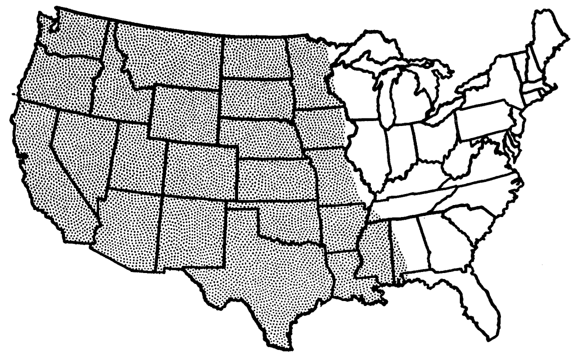

Fig. 5. Distribution of *Euphorbia spatulata* Lam., a subgenus esula species which could serve as a bridge from leafy spurge to the rare spurges under review.

Table 4 lists the native *Euphorbia* spp. used in host specificity testing at the USDA's Albany quarantine. The purpose of the Albany program is to try to predict what the potential host range, within the North American *Euphorbia*, could become if a particular organism was introduced. When a candidate insect comes to Albany, it has been determined to be specific to the genus *Euphorbia* by the overseas testing programs in Rome, Italy, Delemont, Switzerland, or Regina, Canada. Usually few native North American spurges have been tested. The test plants at Albany are selected to represent the four different subgenera (Agaloma, Chamaesyce, Esula, and Poinsettia) of the genus *Euphorbia* which occur in North America. Most of the species (10 or 12) are sympatric with leafy spurge, and 9 of the 12 species could act as bridges to rare review species. *E. purpurea* and *E. telephiodes* are test plants because they are under review and are closely related to leafy spurge (subgenus Esula spp.). *E. maculata, E. supina*, and *E. heterophylla* L. are test plants because they are at times reported as weedy (Dunn 1979). *E. marginata* (snow on the mountain) and *E. corollata* L. (flowering spurge) and *E. heterophylla* (fire plant) are cultivated as ornamentals (Bailey 1951). An effort has been made to select native species that possess a number of the desired characteristics to reduce the number of test species needed.

The Insects

Hyles euphorbiae is a large hawk moth whose larvae are defoliators. The moth, which was first released in North America in 1961, occurs on numerous *Euphorbia* spp. throughout its native Eurasia (W. Europe to northern India) (Harris 1984). During the pre-introduction host specificity testing conducted on the moth, two North American native spurges, *E. maculata* and *E. marginata*, were tested and accepted as hosts (Harris, unpubl. rept.). Harris felt that most species of *Euphorbia* were potential hosts. *E. maculata* belongs to the subgenus Chamaesyce and *E. marginata* is a member of the subgenus Agaloma. This acceptance of members of these subgenera, coupled with ready acceptance of European subgenus Esula species, suggests that despite only two North American spurges being tested, the moth could attack most spurge species on this continent. Table 5 summarizes the known host specificity range for this moth and the other insects which will be discussed. *H. euphorbiae* has recently been found to be established on leafy spurge in Montana (N. Rees, USDA, Bozeman, Mont., pers. comm.) from stocks which probably originally were collected from *E. cyparrissias* L. or *E. seguierana* Necker in Europe (Harris 1984). Additional establishments of the moth have been obtained on leafy spurge in Montana in 1984 (N. Rees, pers. comm.), from material released in 1983, which had been collected by USDA Rome laboratory researchers from *E. waldsteinii* in Hungary.

Chamaesphecia tenthrediniformis (Schifferraüller) (Lepidoptera: Ageriidae), is a clear-wing moth which bores the roots of leafy spurge. In its native Europe, *C. tenthrediniformis* is known from *E. esula sensu stricto* and possibly *E. velenovski* (Harris 1984). In the moth's host specificity testing, *E. marginata* was the only North American spurge tested. It did not support development (Schroeder 1969). Releases of this moth began in 1970 and continued for several years. When establishment failed to occur despite repeated attempts, additional laboratory studies were done. This work showed that the larvae were unable to use the spurge forms that are the main problem (Harris 1984). As mentioned above, the principal leafy spurge is thought to be a hybrid of *E. esula sensu stricto* and *E. waldsteinii* (Dunn and Radcliffe-Smith 1980). Since *C. tenthrideniformis* does not use *E. waldsteinii* even when it grows with acceptable *E. esula* (Harris 1984), *E. waldsteinii* may be contributing some quality to the hybrid which is repellent. It is also possible that some *E. esula* quality, required by the moth, is absent. For whatever reason, *C. tenthrideniformis* appears to be too narrow in its host specificity to attack the hybrids and forms of North American leafy spurge.

Table 4. Native europhorbias used in host specificity testing.

Species	Habit	Subgenus	Sympatric with leafy spurge	Potential bridge	Endangered species	Weed	Ornamental
Euphorbia heterophylla L.	Ann.	poinsettia	X	X		X	X
E. cyathophora Engelm.	Ann.	poinsettia	X	X			
E. maculata L.	Ann.	chamaesyce	X	X		X	
E. serpbyllifolia Pers.	Ann.	chamaesyce	X	X			
E. supina Raf.	Ann.	chamaesyce	X	X		X	
E. robusta (Engelm.) Small	Peren.	esula sec. esula	X	X			
E. spatulata Lam.	Ann.	esula sec. galarrhoei	X	X			
E. purpurea (Raf.) Fernald	Peren.	esula sec. not placed	X		X		
E. telephiodes Chapm.	Peren.	esula sec. ipeccacuahae			X		
E. incisa Engelm.	Peren.	esula sec. esula	possibly				
E. marginata Pursh	Ann.	agoloma	X	X			X
E. corollata L.	Peren.	agoloma	X	X			X

Oberea erythrocephala (Schr.) (Coleoptera: Cerambycidae), is a stem- and root-boring beetle of leafy spurge. It is recorded from a number of perennial *Euphorbia* spp. from south and central Europe through Asia Minor and south Siberia (Harris 1984). Four native North American spurges (*E. corollata* and *E. marginata*, subgenus Agaloma; *E. maculata* and *E. supina* Ait.[2], subgenus Chamaesyce) were test plants in egg transfer experiments. None of these plants supported development (Johnson 1979), which suggests a host plant specificity level below the genus level. Not enough testing was done, however, to predict the degree of use of North American spurges. Since larvae of *O. erythrocephala* overwinter in roots and continue to feed in roots the following spring (Schroeder 1969), this beetle probably would require perennial hosts. Fifty of the 107 spurges native to North America are perennials. Releases of this species began in 1979 and have continued through the past season. Introductions of *O. erythrocephala* collected from *E. cyparissias*, *E. seguierana* and *E. esula* in Europe, have done poorly. The larvae appear to be staying in the roots at least two years instead of the normal one and are producing few adults (only one has been recovered to date) (Harris 1984; N. Rees, pers. comm.). *O. erythrocephala* collected from *E. waldsteinii* in Hungary and released as adults in Montana in 1983, have produced adults in 1984 (N. Rees, pers. comm.).

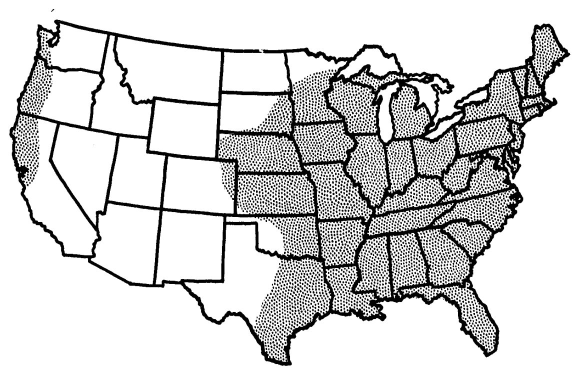

Fig. 6. Distribution of *euphorbia maculata* L., a subgenus chamaesyce species which could serve as a bridge from leafy spurge to rare spurges under review.

Lobesia Euphorbiana (Freyer) (Lepidoptera: Tortricidae), is a tip-webbing moth which is recorded from a number of *Euphorbia* spp. in Europe and Asia Minor. Literature on locality and host records for *L. euphorbiana* are confused because of the presence of *Lobesia occidentalis* Falk., a recently recognized sibling species (Harris and Soroka 1982). Eleven native spurges were tested in the host specificity testing of *L. euphorbiana*. Nine of these species including the subgenus Esula review species *E. purpurea* and *E. telephiodes* appear to support development. (The details of the host specificity testing for *L. euphorbiana* as well as *Bayeria capitigena* [Bremi] [Diptera: Cecidomyiidae] and *Aphthona flava* Guill. [Coleoptera: Chrysomelidae], discussed below, against native spurges will be published elsewhere.) The spurges accepted by this moth represent three of the four *Euphorbia* subgenera present in North America, which contain virtually all the native spurges including the rare species under review. *L. euphorbiana* is a multivoltine insect which develops readily on both annual species and perennial spurges. This moth is cleared for release in Canada. A release of a few moths was made in Saskatchewan in 1983, but no establishment occurred (Maw 1984).

[2] *E. supina* is currently listed (Table 1) as a synonym of *E. maculata* because it was included in the original description of *E. maculata* (USDA, SCS 1982). These plants have frequently been treated as separate species and are probably biologically distinct.

A. flava is a flea beetle, adults of which feed on foliage of leafy spurge and whose larvae feed on and within roots of the plant (Sommer and Maw 1982). This beetle is one of 27 *Aphthona* spp. that have been recorded to be associated with the genus *Euphorbia* in Europe (Sommer and Maw 1982). Three of these species, *A. cyparissiae* (Koch), *A. czwalinae* Weise, and *A. abdominalis* (Duftsch.), are being evaluated for potential use against leafy spurge. *A. flava* is recorded from five perennial *Euphorbia* spp. in its native range, which is from Italy north and east through Austria, Yugoslavia to Bulgaria, Rumania, and Russia (Sommer and Maw 1982). *A. flava* has been tested against 10 native North American *Euphorbia* spp. to try to predict its potential host range. In adult feeding, oviposition and development tests, which are almost complete, it appears that four subgenus *Esula* spp. are acceptable laboratory hosts. The two subgenus *Esula* spp. under review (*E. purpurea* and *E. telephiodes*) were not accepted as hosts. Although development was obtained on the annual species *E. spatulata* (by replacing plants they had killed) *A. flava* would probably need perennial species in nature. From this laboratory testing, it appears that *A. flava* has a host plant specificity level somewhat below the subgenus Esula. Since there are 11 perennial subgenus species, including *E. purpurea* and *E. telephiodes* which appear unacceptable, *A. flava* may be able to use no more than nine native spurges.

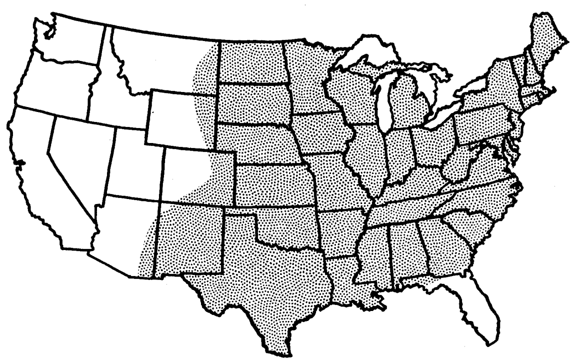

Fig. 7. Distribution of *Euphorbia marginiata* Pursh, a subgenus agaloma species, which could serve as a bridge from leafy spurge to rare spurges under review.

B. capitigena is a midge which galls the meristematic shoot tips of leafy spurge. It is widely distributed in Europe and has been recorded to use at least eight *Euphorbia* spp. in nature (Pecora 1984). In host specificity tests, 11 North American *Euphorbia* spp. were presented to the midges for oviposition and development. The midges laid eggs and completed development to the adult stages on four subgenus *Esula* spp. As with *A. flava*, the review species, *E. purpurea* and *E. telephiodes*, were not accepted as hosts by this midge. *B. capitigena's* level of host plant specificity is probably below the subgenus Esula level. Both annual and perennial species within that group support development and could become hosts for this multivoltine gall midge. Table 5 summarizes the known host specificity levels for the insects which have been discussed.

Discussion

To what degree biological control agents introduced for leafy spurge would use native spurges depends not only on a taxonomic host specificity level and laboratory acceptance, but many other factors including their dispersal ability, habitat preferences, climatic tolerances, and other unknown specifics of both the candidate insects and the potential hosts. Primary among these is the agent's climatic tolerance. This is particularly relevant to their use of non-target native spurges since most of these species are southern in distribution, whereas leafy spurge occurs in the colder parts of North America. Leafy spurge occurs almost entirely above the 0º C mean January isotherm, whereas most of the principal leafy spurge biological control agents (*L. euphorbiana, O. erythrocephala, H. euphorbiae*, *A. flava*, and *B. capitigena*) range south to the climatically mild areas of northern Italy, which is below the 0º C mean January isotherm (Thrower 1968). By matching the temperature data for some of the more southern localities in which the leafy spurge insects live in Europe with comparable places in North America (Walter and Lieth 1967), it could be inferred that these insects probably could live in areas south of the present range of leafy spurge in the U.S., including Texas, and possibly even northern Florida. While this information aids our ability to predict which of the native spurges might become hosts, these predictions are, considering the level of knowledge about both the insects and plants involved, rather simple estimates of risks.

Table 5. Known host plant specificity levels for the leafy spurge insects.

Insect species	No. of native spurges		Subgenus esula	Subgenus agaloma	Subgenus poinsettia	Subgenus chamaesyce	No. of potential hosts	
	tested	*accepted*					native	rare
Hyles Euphorbiae (*L*) (Sphingidae)	2	2	X	X	?	X	<110	<11
Chamesphecia tenthrideniformis (Schif) (Aegeriidae)	1	0	X[1]	?	?	?	may be monophagous	
Oberea erythrocephala (Schrank)(Cerambycidae)	4 partial	0	X	?	?	?	<49	<6
Lobesia euphorbiana (Freyer)(Tortricidae)	11	9[2]	X	X	—	X	<110	<11
Aphthona flava Guill. (Chrysomelidae)	10	4[2]	X	—	—	—	<9	0
Bayeria capitigena (Bremi) (Cecidomyiidae)	11	4	X	—	—	—	<19	1

[1]Subgenus esula acceptance on the basis of leafy spurge (*sensu lato*) feeding.
[2]Species appear to support full development but all testing not completed.

Just what the actual levels of risks are and what damage to or even the elimination of some native spurges would mean are complex issues. These issues relate not only to the scientific possibilities and effects but also to the interest and values of different segments of our society. These issues are explored more fully in Turner (1985).

Whether a native non-target plant can be seriously reduced or eliminated by an introduced biological control agent is a matter of debate. Generally prey-specific ‘predator’ species are not thought to be able to drive their hosts to extinction, if their universe (environment they occupy) is large enough (Huffaker 1958). Extinction is prevented by the so-called density-dependent feedback, which causes the predator population to decline as it reduces its host to rarity. This allows the now rare host to recover. This mechanism breaks down when more than one host is involved since the predator’s population level is no longer regulated by a single prey species. Very large populations of a biological control insect, generated by abundant leafy spurge could swamp a less abundant nearby native spurge, which would have little ability to regulate the agent’s population level. In theory, rare species with restricted habitats would be the most likely to be damaged, since they have the lowest numbers and thus the weakest regulating feedback mechanism.

It has been suggested that the rare spurges will be protected from leafy spurge biological control agents by being difficult to find. The mobility and host-finding abilities of biological control insects, which varies greatly, will determine whether the rare species could be found. *Rhinocyllus conicus* Froelich (Coleoptera: Curculionidae), an introduced biological control insect of *Silybum* and *Carduus* thistles, has successfully colonized rare native *Cirsium* spp. which are quite distant from its weed hosts (Turner, Pemberton, and Rosenthal, USDA Albany, Calif., unpubl. data).

Many insects prefer the rarest of their host plants (Cates 1981). If it is expected that an introduced insect can significantly damage and reduce leafy spurge, to be consistent, it must also be expected that native spurges, which are within the host range of, and exposed to particular introduced insects, could also be damaged and reduced.

The significance of the reduction or loss of native spurges relates to their ecological position, which is poorly known. Since most North American spurge species are small and herbaceous, few figure importantly in the physical structure or energetics of their communities. *E. misera* Benth., a subgenus Agaloma shrub, is considered to be a characteristic component of coastal sage succulent scrub and coastal dunes (Barbour and Major 1977) of southern California and Baja, Mexico. *E. corollata* is listed as a component of the Oak Savanna Community (*Quercus-Andropogon*) of Wisconsin, Minnesota, and North Dakota (Kuchler 1964). The unusual and unique chemistries of spurges suggest their probable involvement in complex ecological interactions. In Europe, where more is known about the ecology of *Euphorbia* spp., there are large numbers of specialist insects, which use *Euphorbia* spp. as hosts, including the unique hemipteran family Stenocephalidae (Miller 1971).

Perhaps more important than the ecological value *per se* are the plants themselves and not their roles. This appears to be the situation with rare and endangered species, which have comparatively fewer environmental interactions and functions. These plants have been given increased value by society at large, via Congressional legislation. The new legal and political value given these plants could have important implications for die biological control approach, if endangered species were to be attacked by biological control agents. Beyond, and yet a part of, the legal concern for species, is a moral concern which relates to the integrity of species. Exponents of this viewpoint say that other life forms have the 'right' to exist and that we should consider and safeguard their welfare, as we go about our activities.

By and large, the concern for species is probably more of a concern for present or potential practical resources for human use, than for the integrity of species. The only native *Euphorbia* spp. which currently have economic value are three ornamentals: *E. corollata* (flowering spurge), *E. marginata* (snow on the mountain) and *E. heterophylla* (fire plant). In northern Mexico, west of the Big Bend area of Texas, is the candelilla wax plant (E. *antisyphilitica* Zucc.), which provides waxes for local consumption and export to the United States (Janick *et al.* 1969). A number of other species in different parts of the world are used for the gums and resins they produce (Schery 1972). Since the advent of the oil crisis, there has been discussion and research on the use of *Euphorbia* spp. as potential energy plants (Calvin 1978). The plants involved thus far (*E. tirucalli* L. and *E. lathyrus* L.) are not native and do not at this point appear to be economically feasible crops (Sachs *et al.* 1981). Some of the native spurges could be economically valuable in the future, considering the energy-rich hydrocarbons, waxes, resins, drying oils, and other useful compounds which are known to occur in some *Euphorbia* spp. The decision to introduce biological control insects to the U.S. rests with a committee of Federal scientists who evaluate the research data on candidate insects, native plant considerations, and the potential effects of the proposed introductions.

Conclusions

Few biological control of weeds projects have the degree of potential use of native plants by introduced insects which occurs in the leafy spurge project. Through selection of target plants for research which have few or no native relatives, this problem can be reduced or avoided. This is not to say that particularly difficult weeds such as leafy spurge, for which there are limited control options, should not become targets for biological control; they can be. It should be expected, however, that plants with large numbers of native relatives will require more research to evaluate host range and other undesirable effects, and that fewer natural enemy options will exist, because of the need for higher levels of host specificity.

There are large differences in the host plant specificity levels of the leafy spurge feeding insects. The research strategy is to select, among these, species which meet two criteria: (1) they are broad enough in host range to accept the diverse forms and hybrids of leafy spurge; and yet (2) narrow enough to exclude use of most native spurges, and the rare species under review in particular.

Neither *C. tenthrediniformis* (which is too narrow in its host range) or *L. euphorbiana* (which is perhaps too broad) seem to be suitable agents for leafy spurge control. It appears however, that both *B. capitigena* and *A. flava,* with host plant specificity levels below the subgenus level, meet these criteria. These insects, and probably other as yet unknown organisms, may begin to reduce leafy spurge abundance and yet allow researchers to remain attentive to the native spurge concerns.

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References

Andres, L.A. 1985. Interaction of *Chrysolina quadrigemina* and *Hypericum* spp. in California. Proc. VI Int. Symp. Biol. Contr. Weeds, August 22-25 1984, Vancouver, Canada. Delfosse, E.S. (ed.). Agric. Can. (in press).

Bailey, L.H. 1951. Manual of Cultivated Plants. MacMillan Pub. Co., NY, 1116 p.

Bakke, A.L. 1936. Leafy spurge, *Euphorbia esula* L. Iowa Agr. Exp. Sta. Res. Bull. 198: 209-45.

Barbour, M.G. and Major, J. 1977. Terrestrial Vegetation of California. John Wiley & Sons, NY, 1002 p.

*Booth, W.E. and Wright, J.C. 1962. Flora of Montana. Part 11. Montana St. College, Bozeman, MT, 280 p. Britton, N.L. 1921. The leafy spurge becoming a pest. J. *NY Bot. Gard.* 22: 73-5.

Calvin, M. 1978. Chemistry, population, resources. Pure and Appl. Chem. 50: 407-25.

Cates, R.G. 1981. Host plant predictability and the feeding patterns of monophagous, oligophagous insect herbivores. Oecologia 48: 319-26.

*Correll, O.S., and Johnston, M.C. 1970. Manual of the Vascular Plants of Texas. Texas Res. Fdn., 1881 p. *Davis, R.J. 1952. Flora of Idaho. Wm. C. Brown, Dubuque, IA, 828 p.

*Dorn, R.D. 1977. Manual of the Vascular Plants of Wyoming. Garland Pub.

Dunn, P.H. 1979. The distribution of leafy spurge (*Euphorbia esula*) and other weedy *Euphorbia* spp. in the United States. *Weed Sci.* 27(5): 509-16.

Dunn, P.H. and Radcliffe-Smith, A. 1980. The variability of leafy spurge (*Euphorbia* spp.) in the United States. N. *Cent. Weed Conf. Res. Rep.* 37: 48-53.

*Gleason, H.A. and Cronquist, A. 1963. Manual of Vascular Plants of Northeastern United States and Adjacent Canada. D. Van Nostrand, Princeton, NJ, 810 p.

Harris, P. 1984. *Euphorbia esula-virgata* complex, leafy spurge and *E. cyparissias* L., cypress spurge (*Euphorbiaceae*). *In:* Biological Control Programs Against Insects and Weeds in Canada 1969-1980. Kelleher, J.S., and Hulme, M.A. (eds.). Commonw. Agric. Bur., pp. 159-69.

Harris, P. and Soroka, J. 1982. *Lobesia* (*Lobesiodes*) *euphorbiana* (Frr.) (Lep.: Oleuthreutinae): A candidate for the biological control of leafy spurge in North America. Can. Dept. of Agric., Regina, Saskatchewan, unpub. rep., 36 p.

*Hitchcock, C.L. and Cronquist, A. 1973. Flora of the Pacific Northwest. Univ. Wash., Seattle, WA, 730 p.

Huffaker, C.B. 1958. Experimental studies on predation: Dispersion factors and predator prey oscillations. Hilgardia 27: 343-83.

Janick, J., Schery, R.W., Woods, F.W., and Ruttan, VW. 1969. Plant Science, and Introduction to World Crops. W.H. Freeman and Co., San Francisco, CA, 629 p.

Johnson, G.R. 1979. *Oberea erythrocephala* larva development - host specificity test 1978-1979. U.S. Dept. Agric., Albany, CA, unpub. rep., 4 p.

*Kearney, T.H. and Peebles, R.H. 1960. Arizona Flora. Univ. of Calif., Berkeley and Los Angeles, CA, 1085 p.

Kuchler, A.W. 1964. Potential natural vegetation of the conterminous United States. Amer. Geogr. Soc. Spec. Pub. No. 36, 155 p.

*Long, R.W. and Lakela, O. 1971. A Flora of Tropical Florida. Univ. of Miami Press, Coral Cables, FL, 962 p.

*Martin, W.C., and Hutchins, C.R. 1980. A Flora of New Mexico. J. Cramer, Hirschberg, Germany, 1276 p.

Maw, M.G. 1984. Status of introductions and main indigenous organisms attacking weeds targeted for biological control in Canada. Can. Dept. of Agric., Regina, Saskatchewan, unpubl. list, 13 p.

Miller, N.C.E. 1971. The biological control of the *Heteroptera.* E.W. Classey L.T.D., Hampton, Middlesex, England, p. 67.

*Munz, P.A. and Keck, D.D. 1970. A California Flora. Univ. Calif., Berkeley and Los Angeles, CA, 1681 p.

*Norton, J.B.S. 1900. A revision of the American species of *Euphorbia* of the section tithymalus occurring north of Mexico. MO Bot. Gard. Rept., Vol. 11: 85-144 + plates 11-52.

Ohwi, J. 1965. Flora of Japan. Smithsonian Institute, Wash., D.C., 1066 p.

Pecora, P. 1984. A petition for the introduction into quarantine for further testing of *Bayeria capitigena* (Bremi) (Dip.: Cecidomyiidae), a potential biocontrol agent of leafy spurge (*Euphorbia esula-virgata* 'complex'). U.S. Dept. of Agric., Rome, Italy, unpubl. rep., 29 p.

Radcliffe-Smith, A. and Tutin, T.G. 1968. *Euphorbia. In:* Flora Europea. Tutin, T.G. (ed.). Cambridge Univ. Press, Vol. 2: 213-6.

Reed, C.F. and Hughes, R.O. 1970. Selected Weeds of the United States. U.S. Dept. Agric. Handb. No. 366, Wash., D.C., 463 p.

*Rydberg, P.A. 1917. Flora of the Rocky Mountains and Adjacent Plains. Pub. by the author, I 110 p.

Sachs, R.M., Low, C.B., MacDonald, J.D., Awad, A.R., and Sully, M.J. 1981. *Euphorbia lathyris:* A potential source of petroleum-like products. Calif. Agric., July-August, 35: 29-32.

Schery, R.W. 1972. Plants for Man. 2nd ed. Prentice-Hall, Englewood Cliffs, NJ, 657 p.

Schroeder, D. 1969. Studies on phytophagous insects of *Euphorbia* spp. *Chamaesphecia empiformis* (Esp.) weed projects for Canada. *Commonw. Inst. Biol. Contr. Prog. Reps.* 22 (21 p.) and 23 (23 p.).

Selleck, G.W. 1959. The autecology of *Euphorbia esula* L. Ph.D. thesis, Dept. Botany, Univ. of Wisconsin, Madison, WI, 309 p.

Selleck, G.W., Coupland, R.T., and Frankton, C. 1962. Leafy spurge in Saskatchewan. Ecol. Monogr. 32: 1-29.

*Small, J.K. 1933. Manual of the Southeastern Flora. Pub. by the author, NY, 1554 p.

Sommer, G. and Maw, E. 1982. *Aphthona cyparissiae* (Koch) and *A. flava* Guill. (Coleop: Chrysomelidae): Two candidates for biological control of cypress and leafy spurge in North America. Commonw. Inst. Biol. Contr. European Sta. Rep., Delemont, Switzerland, 60 p.

Steward, A.N. 1958. Manual of Vascular Plants of the Lower Yangtze Valley China. Oregon State College, Corvallis, OR, 621 p.

*Steyermark, J.A. 1963. Flora of Missouri. Iowa State Univ., Dubuque, IA, 828 p.

Thrower, N.J.W. 1968. Man's Domain, a Thematic Atlas of the World. McGraw Hill Book Co., 76 p.

*Tidestrom, I. 1925. Flora of Utah and Nevada. Contr. U.S. Nat. Herb., Wash. D.C. Vol. 25, 665 p.

Turner, C.E. 1985. Conflicting interests and biological control of weeds. Proc. VI Int. Symp. Biol. Contr. Weeds, August 19-25 1984, Vancouver, Canada. Delfosse, E.S. (ed.). Agric. Can. (in press).

U.S. Department of Agriculture. 1982. National list of scientific plant names. Soil Conserv. Serv. Tech. Pub. 159. Vol. I and III, 854 p.

U.S. Department of the Interior, Fish and Wildlife Service. 1980. Endangered and threatened wildlife and plants: Review of plant taxa for listing as endangered or threatened species. Fed. Regis. 45(242): 82480-569.

U.S. Department of the Interior, Fish and Wildlife Service. 1983. Endangered and threatened wildlife and plants: Supplement to review of plant taxa for listing as endangered or threatened species. Fed. Regis. 48(229): 53640-70.

United States Government Council on Environmental Quality. 1978. National Environmental Policy Act Regulation. Fed. Regis. 43(230): 55978-6007.

Walter, H. and Leith, H. 1960. Klimadiagram Weltatlas. Gustav Fisher, Jena.

*Wheeler, L.C. 1941. *Euphorbia* subgenus Chamaesyce in Canada and the United States exclusive of southern Florida. Rhodora 43.

Wheeler, L.C. 1951. *Euphorbia. In:* Illustrated Flora of the Pacific States. Abrams, L. (ed.). Stanford Univ., CA, Vol. 111: 30-41.

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*These citations were used to compile and summarize data and to prepare the range maps for the *Euphorbia* and *Chamaesyce* spp. in the U.S.