Chapter 24

Biological Control of Leafy Spurge

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NON-TECHNICAL SUMMARY

Leafy spurge, *Euphorbia virgata* (Euphorbiaceae), is a persistent invasive weed causing an expensive management problem that costs U.S. agriculture millions of dollars annually in reduced rangeland productivity and revenue. Chemical control is often only marginally successful, and the repeated applications required carry high economic and ecological costs. In the 1960s, the aggressive spread of leafy spurge led to concerted efforts to develop a biological control program against leafy spurge. Because the weed reproduces both by clonal sprouting and substantial seed production, a long-term, low-input control method was required to impose consistent pressure on the plant and reduce leafy spurge populations to acceptable levels. Today, widespread establishment and biocontrol management with *Aphthona* species of flea beetles (Coleoptera: Chrysomelidae) is a critical component of integrated leafy spurge control across large areas of the western United States.

HISTORY OF INVASION AND NATURE OF PROBLEM

Leafy spurge, *Euphorbia virgata* (Euphorbiaceae), originates from across Europe and western Asia with a center of distribution in the Caucasus (Croizat, 1945; Moore, 1958; Selleck et al., 1962). The first collections of leafy spurge in North America were from Massachusetts in 1827 (Britton, 1921; Bakke, 1936) and Ontario in 1889 (Gusson, 1944), then records show the weed spreading westward to Minnesota in 1890 (Kommedahl and Johnson, 1959), North Dakota in 1909, and California in 1916 (Stevens, 1927; Robbins, 1940). By 1933, it was found coast to coast in the United States and was reported from 19 states (Hanson and Rudd, 1933). Leafy spurge is hypothesized to have arrived in North America via soil used as ship ballast (Britton, 1921) and as a contaminant in oats, wheat, and smooth bromegrass (*Bromus inermis*) seed from Russia and Hungary (Batho, 1931; Dunn, 1985). This weed has likely been introduced multiple times from different regions of Eurasia, as evidenced by the diverse strains and ecotypes that have been noted in North America (Baker and Arnekleu, 1964).

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The first report of the weediness of this species came from an editorial in the New York Herald in 1921 (Feb 9, p. 8). Hanson and Rudd (1933) reported three centers of infestation: one on the east coast; scattered infestations in Montana, Idaho, and Washington; and a large and costly infestation in the northern central prairie regions (**Fig. 1a**). By 1975, leafy spurge was found in 30 states and every province of Canada except Newfoundland (Dunn, 1979; **Fig. 1b**). By the time the first leafy spurge symposium was held in 1979, the weed had invaded an estimated 1 million ha (2.5 million acres), with an associated annual (1978) cost of $10.5 million (Noble, 1979; **Fig. 1c**). Nearly 15 years later, almost 6% of the non-tilled land in North Dakota (approximately 410,000 ha or 1,013,000 acres) was infested with leafy spurge (Leitch et al., 1996). Ten years after that, Duncan et al. (2004) estimated that leafy spurge occupied nearly 1.5 million ha (3.7 million acres) in 17 western states, with an annual spread rate of 12–16%, as well as infesting 400,000 ha (nearly 1 million acres) in the eastern United States. More recent estimates show leafy spurge presence in 37 states (not found in the southeastern United States), and seven Canadian provinces and territories (EDDMapS, 2022; **Fig. 1d**).

Frequent introductions through contaminated seed from Europe and Asia throughout the late 1800s and early 1900s likely laid the foundations for the major invasions in the north-central states and the prairie provinces of Canada (Dunn, 1985). Because leafy spurge invades both cropland and pasture, and because it can establish from seeds, root buds, or root fragments, dispersal through agricultural landscapes was likely common and aided extensively by humans. Seed production peaks around the time of hay harvest in these areas, increasing the potential for movement in hay and forage. Additional dispersal with seed exchange, and through farm equipment and railroads, exacerbated spread, and overgrazing and lack of revegetation left bare soil open for invasion (Selleck et al., 1962; Dunn, 1985; Messersmith et al., 1985). Leafy spurge seeds are physically propelled away from mother plants, ensuring wide distribution in local patches. Seeds are also moved by and germinate in water, which historically led to extensive invasions along waterways (Selleck et al., 1962), and animal dispersal may contribute to over-land movement, though direct evidence is limited (Messersmith et al., 1985). As leaf spurge spread through western North America, land managers attempted to control it by cultivation, manipulating grazing, and applying herbicides, but the invasion continued to double in size approximately every 10 years. Consequently, chemical costs were increasing as well (Anderson et al., 1999). High propensity for both local and long distance spread, as well as the difficulty and longevity of management required to eradicate leafy spurge once established, ensured that this weed remained a priority pest across its introduced range.

WHY CONTROL THIS INVASIVE SPECIES?

Leafy spurge is a perennial, highly self-incompatible forb native to Europe. It grows in dense patches and all parts of the plant contain a milky latex toxic to cattle, which causes cattle to avoid grazing in leafy spurge-infested pastures. The plant also contains phytotoxic compounds that may inhibit competing vegetation (e.g., Qin et al., 2006), although these interactions are not well-studied. Leafy spurge produces extensive root systems that allow it to aggressively outcompete other plants. Impacts on plant communities often persist even after the weed is removed. These invasion legacy effects have been attributed to slow recruitment of desirable species, secondary invasions, or lack of revegetation after control (e.g., Lesica and Hanna, 2009; Larson and Larson, 2010). The intensive management needed to suppress leafy spurge infestations and the residual effects on the soil have long-term effects on the soil microbial community and plant recruitment (e.g., Pritekel et al., 2006; Lesica and Hanna, 2009). Consequently, forage and native species are reduced, and net rangeland productivity declines in invaded areas, reducing cattle production (Hansen et al., 1997; Bangsund et al., 1999; Mangold et al., 2018). Eradications of leafy spurge invasions are unlikely; at best, management primarily reduces weed abundance and impacts to ecologically and economically tolerable levels (Progar et al., 2010). Biocontrol agents, when established at adequate densities, provide necessary enhancements to weed reduction measures. Although leafy spurge remains an important target for control

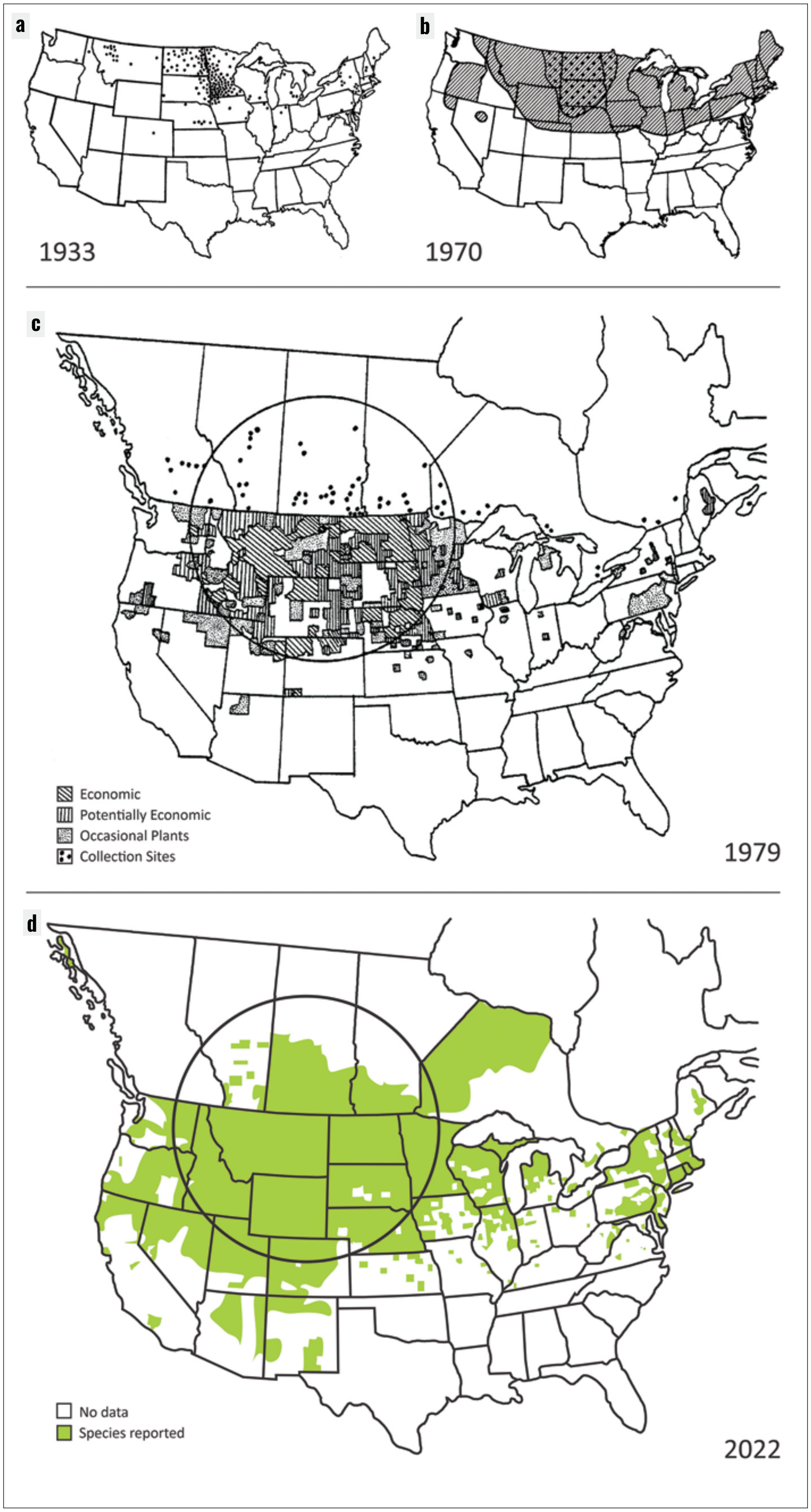

Figure 1. Distribution of leafy spurge (*Euphorbia virgata*) invasions from the 1930s through present day. Hatching reflects different degrees of impact, and the circles in the bottom two figures indicate the region with the highest density of infestations. (modified from a: Hanson and Reed, 1933; b: Dunn, 1979; c: Noble, 1979; d: EDDMapS, 2022)

throughout the western United States (e.g., Van Wychen, 2017; Mangold et al., 2018), it also provides a broadly implemented and well documented example of successful weed biocontrol.

THE ECOLOGY OF THE PROBLEM

Leafy spurge's high reproduction capacity, and the rapidity and intensity with which it becomes entrenched once established, make its control complicated. Frequent root budding and high seed production lead to dense leafy spurge infestations that require several years of intensive effort to manage. More than half of the plant's biomass is often below-ground, and vegetative shoots can emerge from depths of 30 cm (12 in) for several years even if the majority of the root mass is removed. Selleck et al. (1962) estimated that below-ground mass would need to be excavated more than 0.5 m (20 in) deep to have any influence on above-ground biomass. Seeds are dehisced (ejected) from plants to distances of 5 m (16 ft) or more, contributing to site-level spread and reducing the rate at which new plants might be limited by local shoot densities. Seedlings begin producing vegetative buds within seven days after plant emergence. After 10 days, seedlings can survive and resprout from root buds, even if cut to ground level. Patches can reach densities of 200 or more shoots per m^2 (18.6/ft^2), causing declines in forbs and near elimination of annual species in infested areas (Selleck et al., 1962; Messersmith et al., 1985). Moisture availability and seasonal temperatures, and to a lesser degree nutrient availability, influence rates of patch expansion and extent of above-ground cover between years. Individual patch margins are highly variable but often increase at rates of 0.5 to 4 m/year (1.6–13 ft/year), with likely greater expansion below ground. For instance, patches may appear to recede in dry years, but this is not usually associated with below-ground mortality, and vegetative shoots will re-emerge from rootstocks once conditions improve (Selleck et al., 1962). Leafy spurge's high capability for spread and establishment, as well as its tolerance of severe damage and unfavorable conditions, makes eradication generally intractable.

Integrating measures such as herbicide application and grazing can be effective at reducing weed densities, but pressure must be maintained to adequately control infestations and prevent further invasion (Lym, 2005). Leafy spurge's high tolerance of top-kill and above-ground biomass removal, and additional factors such as passive release of herbicides from spurge roots (Hickman et al., 1989), mean that successful chemical control will be temporary unless maintained over a whole season and throughout several subsequent years. For instance, Datta et al. (2013) found that leafy spurge patches began recovering by the third year after treatment. The use of herbicides alone for control is generally not feasible over the long term due to the expense and the cumulative effects on rangeland of the intense herbicide treatments required. Bangsund et al.,(1996) estimated that herbicide treatments for leafy spurge control gave cow–calf operations a positive return only in leafy spurge patches of 0.5 ha (1.2 acre) size or less.

Grazing management, particularly with sheep and goats, reduces leafy spurge top-growth and spread but has limited influence on the root system; new shoots can later be produced, and shoot recruitment can be stimulated by top removal (Lym, 2005). When appropriately timed and trained, targeted grazing might deplete root reserves and reduce infestations, but grazing treatments must be long-term efforts for leafy spurge suppression (Rinella and Bellows, 2016). Bowes and Thomas (1978) reported that more than three years of continuous sheep grazing were required to reduce leafy spurge stem densities, and even after eight years, 5–10 shoots/m^2 (0.5–0.9/ft^2) were being produced by the perennial root systems. Fire may reduce above-ground stems and young plants, but burning is unlikely to substantially harm patches without additional management (Fellows and Newton, 1999). Although most leafy spurge seeds germinate within the first three years after their dispersal, seed dormancy can allow new plants to grow abundantly from a single seed cohort in the seed bank for up to five years, and to some degree for up to 13 years (Selleck et al., 1962). Thus, biological control provides an important and necessary additional tool to maintain suppression pressure of the plant's populations with minimal investment by the landowner in labor or resources (Lym, 1998, 2005).

PROJECT HISTORY THROUGH AGENT ESTABLISHMENT

The low abundance of leafy spurge and high diversity of associated insects found in the plant's native range suggested that classical biological control might be effective in suppressing leafy spurge. Inspired by earlier successful weed biological control projects in western North America, such as the control of St. Johnswort (*Hypericum perforatum*) by species of *Chrysolina* beetles, researchers from CABI (Center for Agriculture and Bioscience International) and the USDA Agricultural Research Service (ARS) European Biological Control Laboratory began work in the 1960s to identify potential candidate biological control agents for leafy spurge. Agent exploration is often done in the center of evolutionary origin of a weed species, which in this case was hypothesized to be the Caucasus Mountains (Croizat, 1945). However, for political and financial reasons, surveys were focused on Hungary, Romania, Austria, and Serbia (Gassman and Schroeder, 1995).

The first attempts at biological control of leafy spurge involved large insects that could do great visible damage to plants in a short time. In 1966, *Hyles euphorbiae* (Lepidoptera: Sphingidae), a hawkmoth from western Europe that can defoliate plants when at high densities, was released in Canada and then in the United States. The hawkmoth was hindered by disease and predation, which lowered its densities. Even when the hawkmoth occurred at high densities, defoliation by this species did not control leafy spurge (Gassman and Schroeder, 1995). Other large insects that were released in the United States in the 1970s and 1980s included three species of *Chamaesphecia* (Lepidoptera: Sesiidae) and the beetle *Oberea erythrocephala* (Coleoptera: Cerambycidae). All three *Chamaesphecia* species are thought to have failed to establish on leafy spurge. *Oberea erythrocephala* did establish, but whether populations reach high enough densities to reduce leafy spurge infestations is still unknown.

Table 1. Biological control agents of leafy spurge (*Euphorbia virgata*) permitted and introduced in the United States. Primary targets are those impacts considered to be the agent's most important effects. The information is summarized from Winston et al., 2014 and Winston et al., 2021. Hosts are either EC (*Euphorbia cyparissiae*) or EV (*Euphorbia virgata*). This list does not include species released only in Canada or only on EC.

Order, Family	Species	Primary damage targets	Primary reproduction target	Hosts
Established				
Coleoptera, Chrysomelidae	*Aphthona cyparissiae* (Koch)[1]	Rootlets/roots	Vegetative Recruitment	EC, EV
Coleoptera, Chrysomelidae	*Aphthona czwalinai* (Weise)[1]	Rootlets/roots	Vegetative Recruitment	EC, EV
Coleoptera, Chrysomelidae	*Aphthona flava* Guillebeau[1]	Rootlets/roots	Vegetative Recruitment	EC, EV
Coleoptera, Chrysomelidae	*Aphthona lacertosa* Rosenhauer[1]	Rootlets/roots	Vegetative Recruitment	EC, EV
Coleoptera, Chrysomelidae	*Aphthona nigriscutis* Foudras[1]	Rootlets/roots	Vegetative Recruitment	EC, EV
Lepidoptera, Sphingidae	*Hyles euphorbiae* (L.)	Foliage	Seed Production	EC, EV
Coleoptera, Cerambycidae	*Oberea erythrocephala* (Schrank)[1]	Stems, Flowering	Seed Production	EV only
Diptera, Cecidomyiidae	*Spurgia capitigena* (Bremi)	Vegetative & flower buds	Seed Production	EC[2], EV
Diptera, Cecidomyiidae	*Spurgia esulae* Gagné[1]	Vegetative & flower buds	Seed Production	EC, EV
Not Established				
Coleoptera, Chrysomelidae	*Aphthona abdominalis* (Duftschmidt)[1]	Rootlets/roots	Vegetative Recruitment	EV only
Lepidoptera, Sesiidae	*Chamaesphecia crassicornis* Bartel	Main roots, stems	Vegetative Recruitment	EV only
Lepidoptera, Sesiidae	*Chamaesphecia hungarica* Tomala[1]	Main roots, stems	Vegetative Recruitment	EV only
Lepidoptera, Sesiidae	*Chamaesphecia tenthrediniformis* (Denis & Schiffermüller)	Main roots, stems	Vegetative Recruitment	EV only

[1] Agents released by APHIS redistribution programs as reported by Hansen et al., 1997.
[2] Establishment documented in Canada only.

The failure of above-ground defoliation by the hawkmoth (*H. euphorbiae*) to control leafy spurge led to a shift in focus towards insects that attack the plant's root system. The spread of leafy spurge at the local (patch) level was thought to come primarily from new shoots arising from lateral roots rather than seed dispersal. The project also shifted towards finding agents with a lower per capita feeding rate but that were present in large numbers. Emphasis was also placed on using many different agents attacking different plant parts, such as the stems or the reproductive structures. Another strategy employed by the program was to look for agents that were effective in particular habitats supporting leafy spurge (Gassman and Schroeder, 1995). A dozen or more species were studied as potential agents, with emphasis on various species of root-feeding *Aphthona* flea beetles (Coleoptera: Chrysomelidae), in part because of the success achieved in other biocontrol projects using beetles in this family. Studies also focused on potential agents from other *Euphorbia* species in Europe. Some of these agents were known to attack, and had been collected from, several *Euphorbia* species. *Euphorbia cyparissias*, for example, was not considered the main target for control in the United States, but this species was invasive in North America, and it ultimately proved to be the source for several agents from Europe. Some insects that were collected from *E. cyparissias* were released against *E. virgata* (mostly in eastern Canada), while other agents were released against both *Euphorbia* species (see Winston et al., 2014, 2021).

In total, 18 species from eight genera were screened for host specificity, approved for release, and subsequently released against leafy spurge in North America. Of these, 11 species are currently considered established in North America. Only 13 of the 18 have been officially introduced to the United States (the remaining five were only introduced to Canada); nine of the 13 species released in the United States have been reported as established (Winston et al., 2014, 2021) (**Table 1**). Five of these nine established agents are species of univoltine *Aphthona* flea beetles that feed on young roots and shoots developing from rootstocks (**Fig. 2**). These five flea beetles were introduced starting in the late 1980s.

The other four established agents include two spurge midges (*Spurgia* spp., Cecidomyiidae) that attack above-ground buds, potentially reducing seed production, the spurge hawkmoth (*H. euphorbiae*),

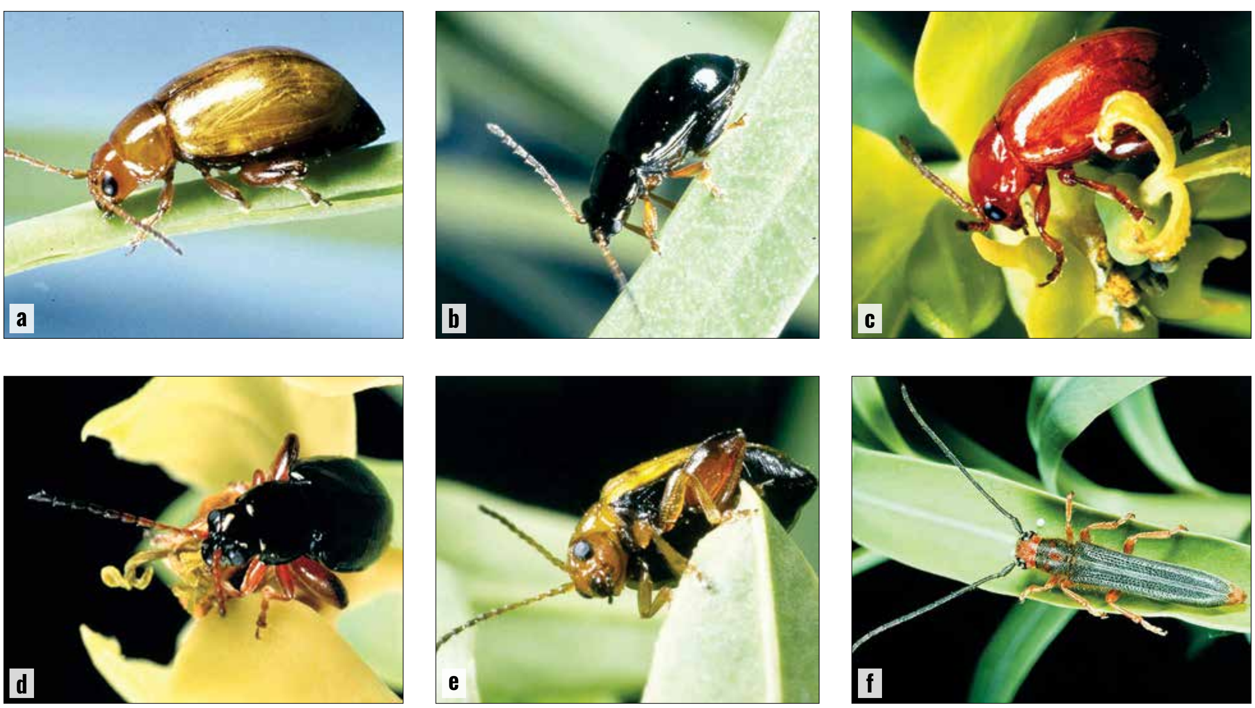

Figure 2. Principal established biocontrol agents for leafy spurge, *Euphorbia virgata*, in the United States. Five of these are flea beetles in the genus *Aphthona* that feed on roots as larvae and above-ground plant parts as adults: (a) *A. cyparissiae*; (b) *A. czwalinai*; (c) *A. flava*; (d) *A. lacertosa*; and (e) *A. nigriscutis*. One additional agent (f) is a stem and root-crown mining beetle, *Oberea erythrocephala*. (a–f: R.D. Richard, USDA-APHIS)

which is a defoliator, and the red-headed stem borer (*O. erythrocephala*) (**Fig. 2f**), which girdles stems and mines the root crown (**Table 1**). The four agents introduced in the United States that failed to establish were a multivoltine flea beetle (*Aphthona abdominalis*) and three species of *Chamaesphecia* moths (**Table 1**).

The various *Aphthona* flea beetle species became widely established and caused dramatic reductions in leafy spurge infestations (**Figs. 3,4**). This success provided the basis for successful leafy spurge biocontrol in North America (Anderson et al., 2003). From the late 1980s to the early 2000s, large-scale release and redistribution programs were funded by the U.S. government, particularly through the USDA-APHIS and ARS, to facilitate the introduction and wide dissemination of these promising biological control agents. These programs were primarily focused on *Aphthona* species, although additional agents, as well as some that subsequently failed, were also released through these efforts. APHIS released seven successful agents and two that failed to establish throughout the Great Plains region between 1988 and 1996 (Hansen et al., 1997) (**Table 1**). More than 48 million biocontrol insects were distributed through an ARS-funded education, outreach, and research program (TEAM Leafy Spurge) (Anderson et al., 2003) that was cooperatively managed by APHIS. In this program, multiple agencies partnered with tribes and private landowners to facilitate releases and the establishment of *Aphthona* insectaries, as well as research on subsequent impacts on leafy spurge (mainly in Montana, Wyoming, North Dakota, and South Dakota). Programs such as these, in combination with state and local distributions, resulted in the widespread establishment of several *Aphthona* species throughout the western United States. For example, of 100 leafy spurge biocontrol release sites surveyed in 2019 in Idaho, Montana, and North Dakota, only five had no *Aphthona* flea beetles present, and these five sites had very low leafy spurge densities (West et al., in review).

In contrast to the successful *Aphthona* species, the relative abundance and fate of the non-*Aphthona* agents in the landscape remains unclear, except for *O. erythrocephala*. Despite variable impacts and uncertain

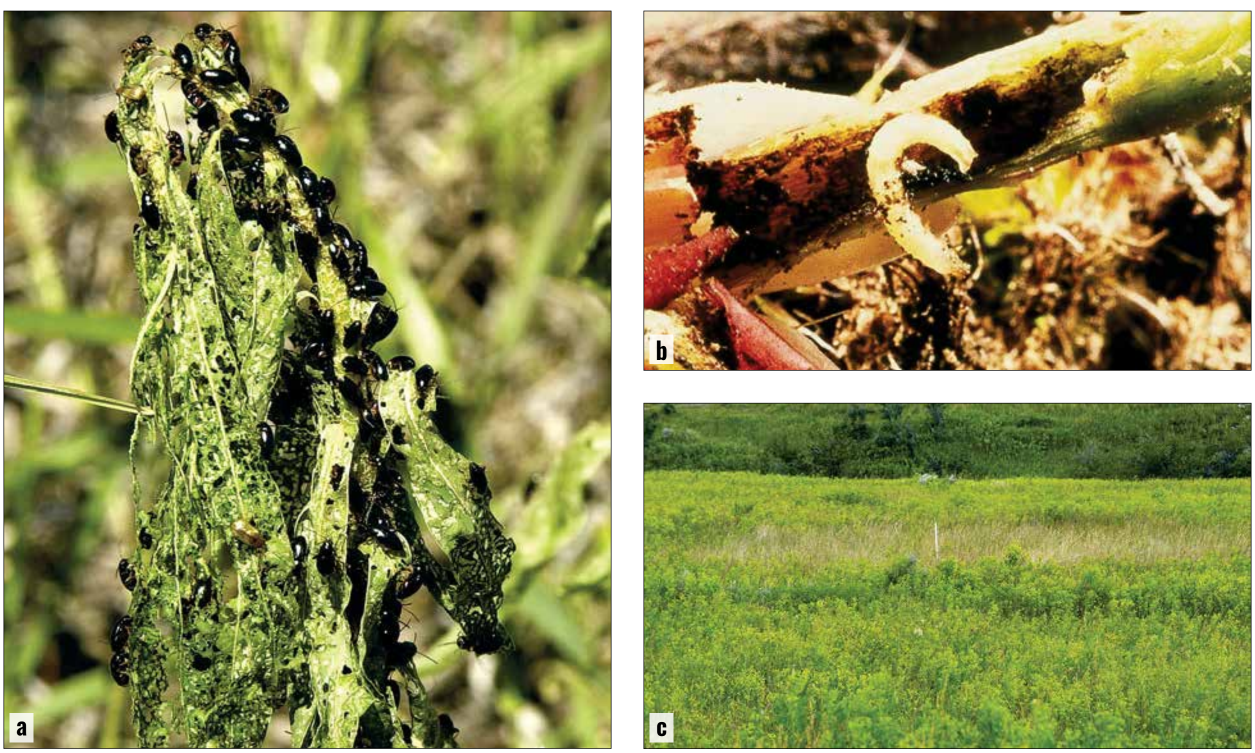

Figure 3. *Aphthona* spp. flea beetle damage and impacts: (a) flea beetle adults attacking a leafy spurge plant; (b) flea beetle larva feeding on roots; (c) Impacts of flea beetles on a leafy spurge infestation. The white pole in the center of the photo is the location of a biocontrol release. Colonization by flea beetles caused high reductions in stem density, resulting in a 'crater' of open habitat within the leafy spurge patch. (a–c: USDA-ARS TEAM Leafy Spurge)

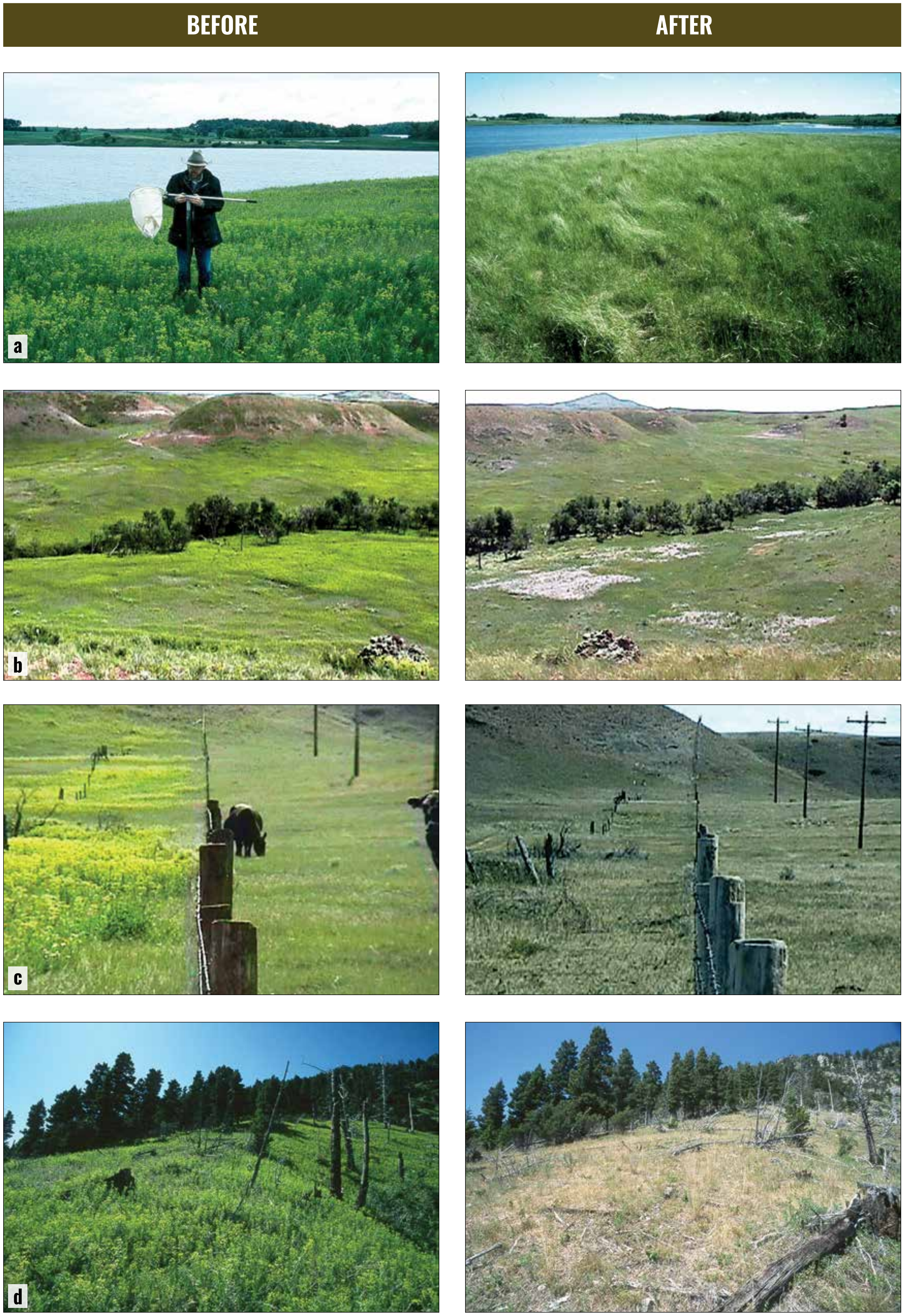

Figure 4. Leafy spurge (*Euphorbia virgata*) infestations before and after the release of *Aphthona* flea beetle agents (a) Lake Ashtabula, ND: herbicides plus *A. czwalinai/ lactertosa* release (pictured: Don Mundal, North Dakota State University); (b) Sentinel Butte, ND: *Aphthona* species plus multi-species grazing; (c) integrated management with *Aphthona* species on the left fenceline; (d) Bridger Mountains, MT: *A. nigriscutis* release. (a–d: USDA-ARS TEAM Leafy Spurge)

abundance early in its introduction (Gassman and Schroeder, 1995), *O. erythrocephala* has independently colonized sites (e.g., Anderson et al., 2015), is commonly encountered, and is being redistributed throughout the northern Great Plains and Rocky Mountain West. For instance, more than 23,000 individuals of this species were moved between 2019 and 2021 by the Montana Biocontrol Coordination Project (N. West, unpub. data; M. Maggio, pers. comm.). However, few field studies have quantified this agent's impact or its current distribution or abundance.

Another agent, the hawkmoth *H. euphorbiae*, is also commonly encountered as a generalist pollinator in grassland communities (e.g., Fox et al., 2013); however, its low impact as a biocontrol agent has made it a low priority for any further monitoring. The two spurge midges are difficult to distinguish, and although *Spurgia* species have been detected in the field (e.g., Lym et al., 1996; Hansen et al., 1997), little is known of their distribution or rates of dispersal. Increased monitoring and sampling across the introduced range of these four agents would be needed to determine their extent and abundance in North America.

HOW WELL DID IT WORK?

The leafy spurge control program has been very successful with its emphasis on *Aphthona* flea beetles (**Fig. 4**). *Aphthona* flea beetles established at >85% of the release sites supported by the TEAM Leafy Spurge project, and flea beetle populations increased seven-fold at the project's demonstration sites in Montana, Wyoming, and North and South Dakota between 1998 and 2000 (Anderson et al., 2003). As a result, leafy spurge cover was reduced by 35 to 100% at different sites over the 2–3 years studied (Anderson et al., 2003). Among the 292 release sites supported by TEAM Leafy Spurge, 91% had quantified reductions in leafy spurge stem density (Samuel et al., 2008). Various studies have recorded observing large flea beetle populations that were associated with reductions in leafy spurge cover that then persisted over time (e.g., Kirby et al., 2000 [revisited in Joshi and Olson, 2009]; Butler et al., 2006 [revisited in Butler and Wacker, 2010]; Cline et al., 2008 [revisited in Setter and Lym, 2013; Thilmony and Lym, 2017]). For instance, Lym (2018) reported leafy spurge remained at very low densities (>90% reduction) after 19 years even in the original control plots established by Cline et al. (2008), where insects were not actively introduced. The widespread, rapid success of the *Aphthona* species complex caused most further research and release efforts to be focused on the establishment, impact, and efficacy of these flea beetles.

Integrating biocontrol with other management tools has been demonstrated to work well in rangelands infested with leafy spurge, and integration yields more consistent biocontrol outcomes. Several studies have shown that combining biological control agents with the use of herbicides and grazing reduces leafy spurge populations relative to reliance on a single tool (Lym, 2005). For instance, initial treatments with fall-applied herbicides in combination with biocontrol reduced leafy spurge density 3–5 years earlier than either technique alone, and infestations continued to be controlled by *Aphthona* for the remaining seven years of observation (Lym and Nelson, 2002).

Adding sheep or goat grazing to areas with well-established *Aphthona* populations further reduced above-ground biomass and seed production of leafy spurge (Jacobs et al., 2006). The advantages of using sheep to manage spurge declines with the size and productivity of the pasture (Bangsund et al., 2001), but the gains offered by the faster reduction in spurge cover from grazing can off-set the additional immediate expenses. Also, timing of control activities can affect their efficacy. Spring herbicide applications or grazing too late into the season reduces adult food availability for the biological control beetles and reduces their populations (Lym, 1998). Long-term reduction in above-ground densities eventually reduces leafy spurge seed banks (Thilmony and Lym, 2017); fire may hasten such reductions by triggering large flushes of germination from these seed banks (Larson et al., 2008). Fire can also improve establishment of *Aphthona*, which seems to be improved by reduced groundcover, and fire does not appear to harm larval survival (Fellows and Newton, 1999; Lym, 2005). Resident communities of other plants respond strongly to biocontrol-driven reductions in leafy spurge cover, but this recovery can be slow, and secondary invasions of other weeds often occur (e.g., Lesica and Hanna, 2009; Larson and Larson, 2010). Flea beetle damage may inhibit replacement of spurge by other species to some degree, perhaps due to persistent below-ground competition even with removal of significant above-ground biomass, or perhaps due to chemicals released by the beetles or damaged leafy spurge in the soil (e.g., Kirby et al., 2000; Cline et al., 2008). Therefore, human-assisted revegetation can help increase plant competition and create conditions less susceptible to re-infestation by leafy spurge. However, the intensive tillage and herbicide applications often used to ensure establishment of seeded forage species are not compatible with establishment of the biocontrol agents (Lym, 2005). Thoughtful multi-step integrated management is important to achieving desired plant communities. *Aphthona* beetles are relatively easy to collect and move, and insectaries for their redistribution have been established for decades in most areas with large infestations. *Aphthona* phenology is well suited to integration with several common management tools in rangeland systems. Biocontrol benefits from an integrated context, which increases the likelihood of long-term sustainable weed control in diverse situations.

Despite their overall efficacy, there are limits and nuances to management with *Aphthona* flea beetles and significant knowledge gaps in their practical use. High leafy spurge stem density, soils composed of greater than 80% sand or that are frequently flooded, and shady sites have all been associated with low *Aphthona* efficacy or establishment (Lym, 1998; Jacobs et al., 2001; Samuel et al., 2008). Although it should be noted that in some instances, inundative releases (50+ *Aphthona* per leafy spurge stem) can overcome some disturbance-related limitations, for instance in riparian zones (Progar et al., 2010). Additional ecological interactions can influence agent efficacy and weed prevalence after *Aphthona* releases, such as the structure and composition of the surrounding habitat (Jonsen et al., 2001; Larson and Grace, 2004), soil conditions, and level of precipitation (Jacobs et al., 2001), as well as host plant genotype and habitat selection pressures on agent assemblages (Lym and Carlson, 2002). *Aphthona* species fail to establish long-term populations with the densities needed for weed management at many sites (Lym, 1998). These failures may reflect the limits of *Aphthona* species' tolerance for particular site conditions, but more subtle factors such as plant tolerance to herbivory or mismatches between agent and host plant genotypes may also play a role.

Biological control agents, under current regulations, must be highly host specific. This host specificity can occasionally reach below the species level and manifest itself as preferences for certain varieties or genotypes of the target plant. Also, the degree to which plants can tolerate or resist attack by agents may vary (Gaskin et al., 2011). Lym and Carlson (2002) showed that leafy spurge plant genotype affected feeding and reproduction of some *Aphthona* species. A study with the midge *Spurgia esulae* found that two plant genotypes from Manitoba and Montana were more resistant to galling than others (Lym et al., 1996). Although female midges laid eggs on all genotypes, egg and larval survival varied among genotypes. For both studies, the work was done on seven plant genotypes, each genotype with a different origin (Manitoba, Montana, Nebraska, North Dakota, South Dakota, Wyoming, and Austria), though it is still unclear if certain genotypes are only found in certain areas. Detailed information about the population structure of this weed, and information on where these genotypes are present across the invaded landscape, could be used to better test agent efficacy.

Additionally, the impacts attributable to each distinct *Aphthona* species in different situations and habitats are usually not known. Multiple *Aphthona* species often were and continue to be released together; they co-occur and are not consistently separated beyond their color groups: black (*A. lacertosa*, *A. czwalinai*) or brown (*A. cyparissiae*, *A. flava*, *A. nigriscutis*). For example, brown flea beetle populations at one point appeared to be nearly all *A. nigriscutis*, and both *A. flava* and *A. cyparissiae* appeared to be scarce. However, genetic analyses found both *A. flava* and *A. cyparissiae* at insectary sites in North Dakota, suggesting this assumption was likely based on a lack of morphological distinction rather than a true absence from the landscape (Roehrdanz et al., 2009). The composition of *Aphthona* agent communities can change after the initial introductions in a location due to differences in mobility and density responses (Larson and Grace, 2004). At some North Dakota sites, high populations of *A. nigriscutis* declined while *A. lacertosa* and *A.*

czwalinai populations increased to the point that they became the most common agents (Lym, 1998). In a Wyoming study, *A. nigriscutis* beetles colonized new areas more quickly than other species, but *A. lacertosa* and *A. czwalinai* survived in greater numbers where either species had been established for a year or more, resulting in a turnover in the relative abundance of agents (Kazmer and Marrs, 2005). Pre-release and native range studies suggest *Aphthona* agents should differ in their habitat preferences (Gassmann et al., 1996; Nowierski et al., 2002). We have limited data on how species composition of the agents has changed over time at individual sites or how differences among agent species have interacted to influence agent community composition or dynamics through time. A rigorous assessment of weed and agent populations and associated habitat conditions would be required to allow management recommendations to be based on releases of particular mixtures of *Aphthona* species.

The other four agents established for leafy spurge biocontrol have not been studied as thoroughly. *Hyles euphorbiae* continues to be considered ineffective, particularly as outbreaks of the agent sufficient to cause severe plant damage are too late in the season to affect the population viability of the weed. This agent's impacts have not been well documented in the recent literature. The two *Spurgia* species are established and have been redistributed with the goal of reducing seed production (Hansen et al., 1997)—especially in wooded areas, which are less favorable for *Aphthona* beetles (Lym, 2005). However, biocontrol with *Spurgia* species requires an integrated approach for success (Lym and Carlson, 1994), and the impact of these agents is likely to be limited by complicated genetics influencing the host-agent interactions (Lloyd et al., 2005; Lym et al., 1996). Another agent, *O. erythrocephala*, co-occurs with *Aphthona* beetles and can cause substantial damage in leafy spurge patches. This combination of agents has worked well and has strong potential to reduce stem densities, and recruitment of both seeds and vegetative propagation. Anderson et al. (2015) reported natural colonization and extensive damage by *O. erythrocephala* at *Aphthona* release sites. In contrast, Progar et al. (2011) saw no impact by *O. erythrocephala* for two years after release, during which there was a reduction in agent abundance. APHIS included the *O. erythrocephala* beetle in its redistribution efforts (Hansen et al., 1997), but this agent did not receive the coordinated efforts expended on the *Aphthona* complex. However, a recent study detected *O. erythrocephala* at approximately ⅓ of 100 *Aphthona* complex release sites surveyed (West et al., in review). This finding, combined with the reported movement of the agent by the current redistribution programs, suggests that *O. erythrocephala* warrants more study to determine its impact on leafy spurge populations and its potential role in leafy spurge biocontrol management.

BENEFITS OF BIOLOGICAL CONTROL OF LEAFY SPURGE

Aphthona biocontrol agents have substantially reduced leafy spurge densities across a wide range of sites and provided sustained control for extensive time periods. Thousands of insects continue to be collected annually from local field insectaries and provided to a diverse range of stakeholders and private landowners on free-collection days (**Fig. 5**). Distribution is further supplemented by similar activities led by various state, tribal, and local entities. A potential benefits estimate made at the beginning of the *Aphthona* release program suggested a possible savings of $59 million per year if the biological control agents could suppress the leafy spurge infestation by 65% by 2025 (Bangsund et al., 1999). We are approaching this date, and although no region-wide estimate is currently available, site-level spurge reductions of this magnitude are not uncommon where *Aphthona* agents have established. Furthermore, surveys conducted during and after the TEAM Leafy Spurge program era suggested biological control had met adopters' expectations and led to favorable changes in land managers' perceptions of the prospects for leafy spurge control (Hodur et al., 2006). Considering that the direct economic impacts of leafy spurge before widespread introductions of *Aphthona* beetles were estimated as $40 million annually in four Great Plains states (Leistritz et al., 2004), the addition of biological control as a low-cost sustained option is undeniably valuable.

Figure 5. Insect giveaway at 'Spurgefest II', held in 2001 at Theodore Roosevelt National Park in Medora, North Dakota. (USDA-ARS TEAM Leafy Spurge)

WORK STILL TO BE DONE

Three specific information gaps still need to be filled: (1) a more detailed taxonomic examination of the weed and the agents; (2) an evaluation of how long-term suppression by agents might require shifts in management targets over time; and (3) a better understanding of agent impacts at a regional scale.

Better Taxonomic Information on the Target Weed

Taxonomic characterization of leafy spurge in North America has always been difficult and contentious. The invasive populations appear to be a complex of species native to Europe and Asia (Croizat, 1945), and there may have been multiple introductions of the various species (Dunn, 1985). Radcliffe-Smith (1985) reported some 20 taxa (species and their hybrids) of leafy spurge in North America. The recent treatment of *Euphorbia* in the Flora of North America (Berry et al., 2021) suggests that *Euphorbia esula* L., a name commonly attributed to the invasion, may have occurred sporadically in North America a century ago, but has not persisted, and in its native range in Europe, *E. esula* has little tendency to be weedy. Berry et al. (2021) suggests that *Euphorbia virgata* Waldst. & Kit. is the correct identification of the leafy spurge invasion. This species is more widespread and weedy in Europe and Asia and is morphologically more like the plants in the North American invasion than other spurge species from Eurasia. There has also been speculation that hybridization and polyploidy may have occurred during the invasion, adding to the confusion (Croizat, 1945; Radcliffe-Smith, 1981; Stahevitch et al., 1988). When agents were selected and tested, researchers lacked sufficient genetic information to provide taxonomic clarity, and current agents were likely collected on *Euphorbia* species or biotypes that are not present in the North American invasive population. A robust clarification of the invasion taxonomy would require molecular analysis to complement the existing chromosomal and morphological classifications. Although the biological control program has been successful in many areas, it is possible that by knowing the genetic identification of the invasive populations in more detail, researchers might be able to find more effective, highly host-specific agents.

Long-Term Effects of Biocontrol on Management Targets

Long-term and widespread herbivore pressure by *Aphthona* species may increase the importance of seed production by reducing the plant's ability to reproduce vegetatively and making competition for germination sites more ecologically important. High genetic diversity, which provides a signature of seedling recruitment in clonal species such as *E. virgata*, is commonly encountered in leafy spurge patches (West et al., in review). This diversity suggests that leafy spurge infestation densities are frequently bolstered by seed production, which may indicate the importance of agents beyond the *Aphthona* species complex. For instance, in-depth research on emerging impacts by *O. erythrocephala* may improve biocontrol management with existing established agents. A better understanding of leafy spurge population dynamics in the landscape would inform management decisions about the degree to which active redistribution of agents that target above-ground structures and additional management to reduce seed production are necessary to manage infestations.

Better Understanding of Agents' Impacts at a Regional Scale

Most published studies on leafy spurge biocontrol agent impact in the United States have documented successful reductions in stem density, but the resulting plant communities (i.e., recovery of native or desirable forbs and forage) have rarely been monitored over the long term. Also, existing impact studies are predominately from north central states (i.e., North Dakota, Montana, and Wyoming). Thus, much of what is known about efficacy of the program in the United States is from studies done at local scales along the habitat gradients of the northern Great Plains ecosystem. Without a large-scale assessment of agent impacts and weed populations, it is difficult to evaluate whether local scale reductions in stem density are truly indicative of broader patterns of leafy spurge population control, or if different agents or supporting measures might be needed in other regions.

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REFERENCES

Anderson, G., E. Delfosse, and N. Spencer. 1999. Biological control of leafy spurge: an emerging success story. *Pest Management Science* 59: 609–613

Anderson, G. L., C. W. Prosser, L. E. Wendel, E. S. Delfosse, and R. M. Faust. 2003. The ecological areawide management (TEAM) of leafy spurge program of the United States Department of Agriculture–Agricultural Research Service. *Pest Management Science* 59: 609–613.

Anderson, J. M., S. A. Willden, L. Dallin, and E. W. Evans. 2015. Long term outcomes of population suppression of leafy spurge by insects in the mountain foothills of northern Utah. *America Midland Naturalist* 174: 1–13.

Baker, L. O. and D. R. Arnekleu. 1964. Variation in leafy spurge strains. Research Progress Report of the Western Weed Control Conference, pp. 10–11. *Western Society of Weed Science Research Committee, Western Weed Control Conference, March 25 – 26, Salt Lake City, UT*. http://www.wsweedscience.org/publications/research-reports/ [Accessed 12 April 2022]

Bakke, A. L. 1936. Leafy spurge, *Euphorbia esula* L. *Iowa Agricultural Experiment Station Research Bulletin* 198: 209–249.

Bangsund, D., F. L. Leistritz, and J. A. Leitch. 1999. Assessing economic impacts of biological control of weeds: the case of leafy spurge in the northern Great Plains of the United States. *Journal of Environmental Management* 56: 35–43.

Bangsund, D. A., J. A. Leitch, and F. L. Leistritz. 1996. Economics of herbicide control of leafy spurge (*Euphorbia esula* L). *Journal of Agricultural and Resource Economics* 21: 381–395

Bangsund, D. A., D. J. Nudell, R. S. Sell, and F. L. Leistritz. 2001. Economic analysis of using sheep to control leafy spurge. *Journal of Range Management* 54: 322–329.

Batho, B. G. 1931. Leafy spurge. Manitoba Department of Agriculture and Immigration Circular No. 106. Manitoba Department of Agriculture and Immigration, Winnepeg, Manitoba.

Berry, P. E., R. Riina, J. A. Peirson, Y. Yang, V. W. Steinmann, D. V. Geltman, J. J. Morawetz, and N. I. Caho. 2021. *Euphorbia*, 237. *In:* Flora of North America Editorial Committee, eds. 1993+. *Flora of North America North of Mexico* (Online]. Vol. 12. http://beta.floranorthamerica.org/Euphorbia. [Accessed 24 September 2021]. New York and Oxford.

Bowes, G. G. and A. G. Thomas. 1978. Longevity of leafy spurge seeds in the soil following various control programs. *Journal of Range Management* 31: 137–140.

Britton, N. L. 1921. The leafy spurge becoming a pest. *Journal of the New York Botanical Gardens* 22: 73–75.

Butler, J. L. , M. S. Parker, and J. T. Murphy. 2006. Efficacy of flea beetle control of leafy spurge in Montana and South Dakota. *Rangeland Ecology and Management* 59: 453–461.

Butler, J. L and S. D. Wacker. 2010. Lack of native vegetation recovery following biological control of leafy spurge. *Rangeland Ecology and Management* 63: 553–563.

Cline, D., C. Juricek, R. G. Lym, and D. R. Kirby. 2008. Leafy spurge (*Euphorbia esula*) control with *Aphthona* spp. affects seedbank composition and native grass reestablishment. *Invasive Plant Science and Management* 1: 120–132.

Croizat, L. 1945. *Euphorbia esula* in North America. *American Midland Naturalist* 33: 231–243

Datta, A., R. E. Rapp, J. E. Scott, L. D. Charvat, J. Zawierucha, and S. Z. Knezevic. 2013. Spring-applied saflufenacil and imazapic provided longer lasting *Euphorbia esula* L. control than fall applications. *Crop Protection* 47: 30–34.

Duncan, C. A., J. J. Jachetta, M. L. Brown, V. F. Carrithers, J. K. Clark, J. M. DiTomaso, R. G. Lym, K. C. McDaniel, M. J. Renz, and P. M. Rice. 2004. Assessing the Economic, Environmental, and Societal Losses from Invasive Plants on Rangeland and Wildlands 1. *Weed Technology*: 18: 1411–1416.

Dunn, P. 1979. The distribution of leafy spurge (*Euphorbia esula*) and other weedy *Euphorbia* spp. in the United States. *Weed Science* 27: 509–516.

Dunn, P. H. 1985. Origins of leafy spurge in North America, pp. 7–13. *In:* Watson, A. K. (ed.). *Leafy Spurge, Monograph Series of the Weed Science Society of America.* Champaign, Illinois, USA.

EDDMapS. 2022. Early Detection & Distribution Mapping System. The University of Georgia - Center for Invasive Species and Ecosystem Health. http://www.eddmaps.org/ [Accessed 29 March 2022].

Fellows, D. P. and W. E. Newton. 1999. Prescribed fire effects on biological control of leafy spurge. *Journal of Range Management* 52: 489–493.

Fox, K., P. Vitt, K. Anderson, G. Fauske, S. Travers, D. Vik, and M. O. Harris. 2013. Pollination of a threatened orchid by an introduced hawk moth species in the tallgrass prairie of North America. *Biological Conservation* 167: 316–324.

Gaskin, J. F., M. C. Bon, M. J. Cock, M. Cristofaro, A. De Biase, R. De Clerck-Floate, C. A. Ellison, H. L. Hinz, R. A. Hufbauer, M. H. Julien, and R. Sforza. 2011. Applying molecular-based approaches to classical biological control of weeds. *Biological Control* 58: 1–21.

Gassmann, A. and D. Schroeder. 1995. The search for effective biological control agents in Europe: history and lessons from leafy spurge (*Euphorbia esula* L.) and cypress spurge (*Euphorbia cyparissias* L.). *Biological Control* 5: 466–477.

Gassmann, A., D. Schroeder, E. Maw, and G. Sommer. 1996. Biology, ecology, and host specificity of European *Aphthona* spp.(Coleoptera, Chrysomelidae) used as biocontrol agents for leafy spurge, *Euphorbia esula* (Euphorbiaceae), in North America. *Biological Control* 6: 105–113.

Gusson, H.T. 1944. Canadian weed survey. First report 1942. Dominion of Canada, Department of Agriculture, Ottawa, Canada.

Hansen, R. W., R. D. Richard, P. E. Parker, and L. E. Wendel. 1997. Distribution of biological control agents of leafy spurge (*Euphorbia esula* L.) in the United States: 1988–1996. *Biological Control* 10: 129–142.

Hanson, H. C. and V. E. Rudd. 1933. Leafy spurge: Life history and habits. Agricultural Experiment Station, North Dakota Agricultural College, Fargo, North Dakota.

Hickman, M. V., C. G. Messersmith, and R. G. Lym. 1989. Picloram release from leafy spurge (*Euphorbia esula*) roots in the field. *Weed Science* 37: 167–174.

Hodur, N. M., F. L. Leistritz, and D. A. Bangsund. 2006. Biological control of leafy spurge: utilization and implementation. *Rangeland Ecology and Management* 59: 445–452.

Jacobs, J. S., R. L. Sheley, and J. J. Borkowski. 2006. Integrated management of leafy spurge-infested rangeland. *Rangeland Ecology and Management* 59: 475–482.

Jacobs, J. S., R. L. Sheley, N. R. Spencer, and G. Anderson. 2001. Relationships among edaphic, climatic, and vegetation conditions at release sites and *Aphthona* nigriscutis population density. *Biological Control* 22: 46–50.

Jonsen, I.D., R. S. Bourchier, and J. Roland 2001. The influence of matrix habitat on *Aphthona* flea beetle immigration to leafy spurge patches. *Oecologia* 127: 287–294.

Joshi, A. and D. L. Olson. 2009. Revisiting leafy spurge biocontrol: a case study. *Rangelands* 31: 31–35.

Kazmer, D. J., and R. W. Marrs. 2005. Assessing long-term impacts of leafy spurge biological control agents: conclusions from a 6-year study. Project report to USDA-APHIS 5179 #58-5436-1-221. https://www.cbd.int/invasive/doc/meetings/isaem-2015-01/BIOCONTROL/iasem-usa-bio-10-en.pdf

Kirby, D. R., R. B. Carlson, K. D. Krabbenhoft, D. Mundal, and M. M. Kirby. 2000. Biological control of leafy spurge with introduced flea beetles (*Aphthona* spp.). *Journal of Range Management* 53: 305–308.

Kommedahl, T. and H. G. Johnson. 1959. Pesky plants. University of Minnesota Agricultural Extension Service Bulletin No. 287. Minneapolis and Saint Paul, Minnesota, USA.

Larson, D. L. and J. B. Grace 2004. Temporal dynamics of leafy spurge (*Euphorbia esula*) and two species of flea beetles (*Aphthona* spp.) used as biological control agents. *Biological Control* 29: 207–214.

Larson, D. L., J. B. Grace, and J. L. Larson. 2008. Long-term dynamics of leafy spurge (*Euphorbia esula*) and its biocontrol agent, flea beetles in the genus *Aphthona*. *Biological Control* 47: 250–256.

Larson, D.L. and J. L. Larson. 2010. Control of one invasive plant species allows exotic grasses to become dominant in northern Great Plains grasslands. *Biological Conservation* 143: 1901–1910.

Leistritz, F. L., D. A. Bangsund, and N. M. Hodur. 2004. Assessing the economic impact of invasive weeds: The case of leafy spurge (*Euphorbia esula*). *Weed Technology* 18: 1392–1395.

Lesica, P. and D. Hanna. 2009. Effect of biological control on leafy spurge (*Euphorbia esula*) and diversity of associated grasslands over 14 years. *Invasive Plant Science and Management* 2: 151–157.

Leitch, J. A., F. L. Leistritz, and D. A. Bangsund. 1996. Economic effect of leafy spurge in the upper Great Plains: methods, models, and results. *Impact Assessment* 14: 419–433.

Lloyd, C. J., R. A. Hufbauer, A. Jackson, S. J. Nissen, and A. P. Norton. 2005. Pre-and post-introduction patterns in neutral genetic diversity in the leafy spurge gall midge, *Spurgia capitigena* (Bremi) (Diptera: Cecidomyiidae). *Biological Control* 33: 153–164.

Lym, R.G. 1998. The biology and integrated management of leafy spurge (*Euphorbia esula*) on North Dakota rangeland. *Weed Technology* 12: 367–373.

Lym, R. G. 2005. Integration of biological control agents with other weed management technologies: successes from the leafy spurge (*Euphorbia esula*) IPM program. *Biological Control* 35: 366–375.

Lym, R. G. 2019. Leafy spurge (*Euphorbia esula*) control and soil seed bank composition 19 years after release of *Aphthona* spp. biological control agents. *In:* Hinz, H. L., et al. (eds.). *Proceedings of the XV International Symposium on Biological Control of Weeds, pp. 269, Engelberg, Switzerland 26–31 August 2018*. FHAAST-2018-06, USDA Forest Service, Morgantown, West Virginia, USA. https://www.ibiocontrol.org/proceedings/

Lym, R. G. and R. B. Carlson. 1994. Effect of herbicide treatment on leafy spurge gall midge (*Spurgia esulae*) population. *Weed Technology* 8: 285–288.

Lym, R.G. and R. B. Carlson. 2002. Effect of leafy spurge (*Euphorbia esula*) genotype on feeding damage and reproduction of *Aphthona* spp.: implications for biological weed control. *Biological Control* 23: 127–133.

Lym, R. G. and J. A. Nelson. 2002. Integration of *Aphthona* spp. flea beetles and herbicides for leafy spurge (*Euphorbia esula*) control. *Weed Science* 50: 812–819.

Lym, R. G., S. J. Nissen, M. L. Rowe, D. J. Lee, and R. A. Masters. 1996. Leafy spurge (*Euphorbia esula*) genotype affects gall midge (*Spurgia esulae*) establishment. *Weed Science* 44: 629–633.

Mangold, J. M., K. B. Fuller, S. C. Davis, and M. J. Rinella. 2018. The economic cost of noxious weeds on Montana grazing lands. *Invasive Plant Science and Management* 11: 96–100.

Messersmith, C. G., R. G. Lym, and D. Galitz. 1985. Biology of leafy spurge, pp. 42–56. *In:* Watson, A. K. (ed.) *Leafy Spurge, Monograph Series of the Weed Science Society of America.* Champaign, Illinois, USA.

Moore, R. J. 1958. Cytotaxonomy of *Euphorbia esula* in Canada and its hybrid with *Euphorbia cyparissias*. *Canadian Journal of Botany* 36: 547–559.

Noble, D. L., P. H. Dunn, and L. A. Andres. 1979. The leafy spurge problem, pp. 8–15. *In: Proceedings: Leafy Spurge Symposium, 26–27 June 1979 Bismark, North Dakota.* North Dakota State University Cooperative Extension Service et al., Fargo, North Dakota, USA.

Nowierski, R. M., Z. Zeng, D. Schroeder, A. Gassmann, B. C. FitzGerald, and M. Cristofaro. 2002. Habitat associations of *Euphorbia* and *Aphthona* species from Europe: development of predictive models for natural enemy release with ordination analysis. *Biological Control* 23: 1–17.

Pritekel, C., A. Whittemore-Olson, N. Snow, and J. C. Moore. 2006. Impacts from invasive plant species and their control on the plant community and belowground ecosystem at Rocky Mountain National Park, USA. *Applied Soil Ecology* 32: 132–141.

Progar, R. A., G. Markin, J. Milan, T. Barbouletos, and M. J. Rinella. 2010. Inundative release of *Aphthona* spp. flea beetles (Coleoptera: Chrysomelidae) as a biological "herbicide" on leafy spurge in riparian areas. *Journal of Economic Entomology* 103(2): 242–248.

Progar, R. A., G. Markin, J. Milan, T. Barbouletos, and M. J. Rinella. 2011. Population dynamics and impacts of the red-headed leafy spurge stem borer on leafy spurge (*Euphorbia esula*). *Invasive Plant Science and Management* 7: 183–188.

Qin, B., L. G. Perry, C. D. Broeckling, J. Du, F. R. Stermitz, M. W. Paschke, and J. M. Vivanco. 2006. Phytotoxic allelochemicals from roots and root exudates of leafy spurge (*Euphorbia esula* L.). *Plant Signaling & Behavior* 1: 323–327.

Radcliffe–Smith, A., 1985. Taxonomy of North American leafy spurge, pp. 14–25. *In:* Watson, A. K. (ed.). *Leafy Spurge, Monograph Series of the Weed Science Society of America.* Champaign, Illinois, USA.

Rinella, M. J. and S. E. Bellows. 2016. Evidence-targeted grazing benefits to invaded rangelands can increase over extended time frames. *Rangeland Ecology and Management* 69: 169–172.

Robbins, W. W. 1940. Alien plants growing without cultivation in California. University of California, College of Agriculture Experimental Station Bulletin No. 637. Berkeley, California, USA.

Roehrdanz, R., D. Olson, G. Fauske, R. Bourchier, A. Cortilet, and S. Sears. 2009. New DNA markers reveal presence of *Aphthona* species (Coleoptera: Chrysomelidae) believed to have failed to establish after release into leafy spurge. *Biological Control* 49: 1–5.

Samuel, L. W., D. R. Kirby, J. E. Norland, and G. L. Anderson. 2008. Leafy spurge suppression by flea beetles in the Little Missouri drainage basin, USA. *Rangeland Ecology and Management* 61: 437–443.

Selleck, G., R. Coupland, and C. Frankton. 1962. Leafy spurge in Saskatchewan. *Ecological Monographs* 32: 1–29.

Setter, C. M. and R. G. Lym. 2013. Change in leafy spurge (*Euphorbia esula*) density and soil seedbank composition 10 years following release of *Aphthona* spp. biological control agents. *Invasive Plant Science and Management* 6: 147–160.

Stahevitch, A. E., C. W. Crompton, and W. A. Wojtas. 1988. Cytogenetic studies of leafy spurge, *Euphorbia esula*, and its allies (Euphorbiaceae). *Canadian Journal of Botany* 66: 2247–2257.

Stevens, O. A. 1927. North Dakota weeds. North Dakota Agricultural College, Agricultural Experiment Station Bulletin No. 162, Fargo, North Dakota, USA.

Thilmony, B. M. and R. G. Lym. 2017. Leafy spurge (*Euphorbia esula*) control and soil seedbank composition fifteen years after release of *Aphthona* biological control agents. *Invasive Plant Science and Management* 10: 180–190.

Van Wychen, L. 2017. Survey of the most common and troublesome weeds in grass crops, pasture and turf in the United States and Canada. Weed Science Society of America National Weed Survey Dataset. Weed Science Society of America, Westminster, Colorado, USA. https://wssa.net/wp-content/uploads/2017-Weed-Survey_Grass-crops.xlsx.

West, N. M., J. F. Gaskin, J. Milan, and T. A. Rand. 2022 High genetic diversity in the landscape suggests frequent seedling recruitment by *Euphorbia virgata* Waldst. & Kit. (leafy spurge) in the northern U.S.A. *Biological Invasions* (in review)

Winston, R. R., C. Bell Randall, R. de Clerck-Floate, A. McClay, J. Andreas, and M. Schwarzländer. 2014. Field Guide for the Biological Control of Weeds in the Northwest. USDA Forest Service Forest Health Technology Enterprise Team Publication FHTET-2014-08. https://bugwoodcloud.org/resource/pdf/Field_Guides_Series/Weeds_of_the_Northwest.pdf

Winston, R. L., M. Schwarzländer, H. L. Hinz, M. D. Day, M. J. W. Cock, and M. H. Julien (eds.). 2021. Biological Control of Weeds: A World Catalogue of Target Weeds and Their Agents. Based on FHTET-2014-04. USDA Forest Service, Morgantown, West Virginia, USA. https://www.ibiocontrol.org/catalog/ [Accessed 30 December 2021].