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LEAFY SPURGE—A REVIEW

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ABSTRACT

Leafy spurge (Euphorbia esula L.) is a perennial herbaceous weed that infests millions of acres of range and pasture in the northern Great Plains. It outcompetes grasses and lowers land productivity because cattle will not graze infested areas even if spurge makes up only 10% of the vegetative biomass. This presentation will cover the history, taxonomy, and phenology of leafy spurge. A discussion of chemical, mechanical, and biocontrol techniques that aid in leafy spurge management will also be included.

REVIEW

Leafy spurge (Euphorbia esula L.) is a highly variable plant or plant group that is found in several countries including Hungary, Austria, Italy, and Russia. It has been introduced several times and at different places in the United States and Canada (Dunn, 1985). Dunn (1985) speculated that leafy spurge was introduced first in ship ballast with the earliest specimens collected in 1877 near Philadelphia. The North American introductions were probably from several separate sites in Europe. Probable sources of Midwestern introductions are immigrant Mennonite seed, Russian seed grain shipments, and brome grass seed (Dunn, 1985).

Thirty of the 48 contiguous United States are infested with leafy spurge (Dunn, 1979). The states where leafy spurge is considered a problem include: Colorado, Idaho, Minnesota, Montana, Nebraska, North Dakota, Oregon, South Dakota, Wisconsin, and Wyoming (Watson, 1985). In 1979, the total area of leafy spurge infestation in the United States and Canada was estimated to be 1,000,000 ha (Noble et al., 1979). A 1989 South Dakota Department of Agriculture survey estimated 61,000 ha (151,000 acres) in South Dakota were infested with leafy spurge, a 9% increase from 1988 (Clarke, personal communication), and a 250% increase from the 1979 estimate of 24,000 ha (60,000 acres) (Noble et al., 1979).

TAXONOMY

Croizat (1945) and Radcliffe-Smith (1985), among others, have discussed the taxonomic problem of classifying the E. esula complex. To date, a definitive relationship has not been established between the North American leafy spurge and the Eurasian species. Ebke and McCarty (1983) did a nursery study and concluded that the majority of leafy spurge plants are actually E. x pseu-
dovirgata, a hybrid between E. esula and E. virgata. The growth of North American leafy spurge was highly variable with some populations having more E. esula characteristics, some having more E. virgata characteristics, but most populations possessed characteristics of both species.

Stahevitch et al. (1988) examined leafy spurge populations for breeding barriers to determine if North American leafy spurge comprised a single breeding population. All E. esula samples were hexaploid, accessions from Europe and different regions in North America were successfully crossed, and pollen stainability was 100% for almost all samples. These results support the concept of a single, polymorphic species.

A number of chemotaxonomic studies also have been done to resolve the leafy spurge taxonomic problems (Manners and Davis, 1984; Harvey et al., 1988; Stahevitch et al., 1988; and Valcarce et al., 1989). The results of these studies have either concurred that leafy spurge is one variable species or been inconclusive. Manners and Davis (1987) discovered differences in leafy spurge accessions using the distribution of di- and triterpenoids occurring in the latex of Euphorbia. They suggested that jatrophane diterpenes, secondary metabolites possibly unique to Euphorbia spp., have considerable taxonomic importance.

Holden and Mahlberg (1992) studied qualitative and quantitative triterpenoid content in leafy spurge latex by gas-liquid chromatography. Relationships between 39 North American and 37 European accessions were examined with the goal of identifying European populations of leafy spurge that supported natural enemies most likely to accept North American leafy spurge as a host. The results showed two things. First, European leafy spurge was much more variable than North American leafy spurge, indicating North American leafy spurge may have arisen from relatively few introductions. The other noteworthy result was that eight leafy spurge accessions from Montana, North Dakota, and South Dakota were most closely related to an accession from near Pest, Hungary.

With the same goal in mind as Holden and Mahlberg (1992) but using a different approach, Nissen et al. (1992) analyzed restriction fragment length polymorphisms (RFLPs) of chloroplast DNA (cpDNA) from two North American and three European leafy spurge accessions to measure genetic variation and relatedness. Results from this study showed that accessions from Russia and Montana were identical to each other and were only slightly different from a Nebraska accession. An Austrian accession was most divergent. These data suggest that biocontrol organisms taken from where the Russian leafy spurge accession was found may be preadapted to the Montana and Nebraska accessions.

PHENOLOGY

The biological significance of leafy spurge is in part due to the phenoology of the plant. Leafy spurge shoots developing from adventitious shoot buds on the root crown and lateral roots emerge early in the spring (early to late April depending on latitude). Seeds may germinate throughout the growing season
if adequate moisture is present. However, germination most commonly occurs in the months of April and May (Selleck et al. 1962). Initiation of the inflorescence occurs within 5-7 days of the shoot's emergence (Selleck et al., 1962) although flowering begins approximately one month after shoot emergence. Yellow bracts that subtend the inflorescence are highly visible during flowering in late May and June. Flowering at the terminal inflorescence lasts about one month but additional branches may continue to flower throughout the summer if conditions are favorable (Messersmith et al., 1985). Seed formation and maturation continues for about 30 days after the last flower appears (Best et al., 1980). Seeds are dispersed as capsules dry and dehisce. Senescence in the fall is characterized by the leaves and stem turning red or yellow with most leaves senescing before a killing frost (Messersmith et al., 1985).

**PLANT BODY**

A mature leafy spurge stem is herbaceous, but woody in texture (Bakke, 1936), and may grow to a height of 90 cm (Selleck et al., 1962). In cross section a majority of the stem is comprised of woody, secondary xylem with a relatively insignificant amount of vascular tissue that surrounds a central pith. To the outside of the vascular cambium is a tight layer of phloem, latex vessels, and periderm. The outer layer of the periderm, along with a heavy cuticle, protect the stem from water loss (Bakke, 1936).

The waxy, linear leaves of leafy spurge have an alternate arrangement except for the first two pairs of leaves of a seedling, which are opposite (Raju, 1985). Leafy spurge leaves are adapted for xeric conditions with sunken stomata on the upper and lower leaf surfaces (Bakke, 1936) and a heavy crystal-like waxy cuticle to prevent water loss (Galitz and Davis, 1983).

The vast, spreading root system of leafy spurge is often cited as the key to the "weediness" of leafy spurge (Best et al., 1980; Derscheid et al., 1985; Raju et al., 1963). Selleck et al. (1962) calculated the mass of leafy spurge roots in 0.4 ha, 1.2 m deep to be 3823 kg of plant material. Raju et al. (1963) described the morphology of the leafy spurge root system as heterorhizic, which is the presence of a dimorphic pattern of root growth. Long and short roots are present, although both types may be difficult to recognize in mature plants because the short root growth is determinate (Raju, 1985). The degree of terminal growth and branching, and the presence of secondary growth distinguishes long from short roots. Only the long roots are important in vegetative propagation through bud formation (Raju et al., 1963).

A cross-section of a young leafy spurge root would reveal a typical arrangement of tissue with a central stele surrounded by cortex and an epidermis (Bakshi and Coupland, 1959). As secondary xylem and phloem are produced, the pericycle becomes meristematic and produces a phellogen layer. Cork is produced on the periphery of the phellogen and phellemid is produced inside this layer. With the secondary growth and production of cork, the outer cortex and epidermis die and slough off (Myers et al., 1964). Mature leafy spurge roots are protected from dry conditions by the cork (Selleck et al., 1962) that varies from 2 to 7 cells in thickness (Bakshi and Coupland, 1959).
Secondary growth produces parenchyma that serves as storage tissue. Laticiferous tissue is abundant throughout the secondary cortex of mature roots (Raju, 1985).

Leafy spurge plants produce axillary and adventitious shoot buds (Raju, 1985). Axillary buds increase branching of aboveground shoots. Adventitious buds found on the roots can be classified as reparative or additional buds (Raju et al., 1963). Reparative buds are produced after an injury while additional buds are produced spontaneously. Bakke (1936) found buds on roots at a depth of 2 m. The number of buds present per unit length of root is greatest just beneath the soil surface and decreases with increasing depth (Coupland and Alex, 1955). Buds counted by depth averaged almost 3 per centimeter in the top 2.5 cm layer of soil. This gradually decreased to approximately 1 bud per 2 cm at the 30 cm layer. The number of buds per unit length of root was found to be positively correlated with the weight of root tissue. With respect to the soil profile, 62% of the buds were found within the A-horizon (Coupland and Alex, 1955).

The ability of an adventitious bud to produce a new shoot is not related to size or placement on the root system. Root bud dormancy control is correlative (enforced by main shoot) rather than innate (Nissen and Foley, 1987). Buds present on the root crown are less susceptible to freezing than buds from root sections (Schimming and Messersmith, 1988). Root crown buds could be expected to endure colder temperatures during the winter than buds on root sections deeper in the soil. Therefore, the ability of leafy spurge buds to resist freezing appears to be correlated with the probability of experiencing the coldest temperatures during winter.

FLOWERING; SEED PRODUCTION AND DISPERSAL

Leafy spurge produces flowers in terminal umbels at the stem apex and on axillary branches (Raju, 1985). The cyathium, a type of flower unique to the genus *Euphorbia*, possesses a single pistil with a compound ovary which is surrounded by 12 to 20 staminate flowers. The pistillate and staminate flowers are surrounded by a cup-shaped involucre. The cyathium is enclosed by five yellow involucral bracts and four nectar glands (Messersmith et al., 1985).

Wind may cause pollination through incidental contact of pistillate and staminate flowers but not through the transport of pollen (Selleck et al., 1962). The presence of nectaries attracts insects to leafy spurge flowers. A survey in Saskatchewan listed 60 insect species associated with leafy spurge during late June and early July of 1955 (Best et al., 1980). Insect feeding on nectar and pollen causes most leafy spurge pollination (Messersmith et al., 1985).

The leafy spurge capsule develops from a superior, 3-celled ovary possessing a central placenta. The capsule, as described by Bakke (1936), has walls with three layers of tissue. The inner layer of contractile tissue is comprised of 3 layers of columnar cells arranged longitudinally. The middle layer is made up of a single layer of parenchymatous cells arranged in a radial fashion. Cells in the outer layer are arranged horizontally toward the lodiculate suture. The mature capsule dehisces explosively, projecting seeds up to 4.5 m
when dried by high temperatures and low humidity (Bakke, 1936). A maximum of 426 seeds/shoot resulting in a seed yield of 3800 kg/ha has been observed (Selleck et al., 1962).

Animals may serve as agents of leafy spurge seed dispersal. Bakke (1936) claimed that mourning doves (*Zenaida macroura* L.) fed almost exclusively on leafy spurge seed if abundant. Mourning doves have the potential to be an efficient seed dispersal mechanism if intact seeds pass through the digestive tract. Bakke (1936) examined 14 doves and found that no seed from the digestive tract was viable, although 17% of seed from the bird’s crop was viable. Blockstein et al. (1987) also found no intact leafy spurge seed in the digestive tract of seven wild mourning doves. They examined fecal material from nests and found viable leafy spurge seed in some nests. Therefore, the primary way leafy spurge seed may be dispersed by mourning doves is by mature doves carrying seed to nestlings, which may not be able to digest the seed as effectively as mature birds.

Ants also have been suggested to be leafy spurge seed dispersal agents. The fleshy caruncle of the leafy spurge seed has led to the suggestion that leafy spurge seed is myrmecochorous (Selleck et al., 1962). Myrmecochory is a type of mutualism between ants and plant species with seeds bearing caruncles or elaiosomes. In this relationship, the ants feed on the elaiosomes and discard the viable seed about the nest. The possible advantages of this relationship to the plant includes: escape of seed predation, competition avoidance, the availability of favorable substrate for germination, and escape from fire (Pemberton, 1988). While Selleck et al. (1962) found no suggestion of myrmecochory in two genera of ants (*Formica* sp. and *Lasius* sp.), Pemberton (1988) reported a myrmecochorous relationship between leafy spurge and *Formica obscuripes*.

Leafy spurge seed may remain dormant for 5-8 years (Messersmith et al., 1985) with viability decreasing each year (Selleck et al., 1962). Temperature appears to be the most important factor influencing leafy spurge seed germination. Early spring germination following several days of 26-28º C maximum air temperature (Selleck et al., 1962) is the norm, with germination through mid-October dependent upon plentiful moisture (Selleck et al., 1962; Best et al., 1980; and Messersmith et al., 1985). Seedling emergence is possible from a depth of 15 cm despite the small seed size (Selleck et al., 1962). In competition with other plants, leafy spurge seedlings undergo severe mortality and rarely produce more than one shoot (Selleck et al., 1962) which almost never produces an inflorescence the first year (Messersmith et al., 1985). However, the seedlings do produce crown buds at the six-leaf stage and these buds are capable of regrowth. Nine of 15 six-leaf seedlings with stems cut off above the buds produced new shoots (Selleck et al., 1962).

**LATEX**

Leafy spurge produces a latex which is exuded from the plant upon injury. The latex is a white fluid containing a serum with a mixture of compounds in solution or suspension (Lynn and Clevette-Radford, 1987). Some of the common components of latex include enzymes, carbohydrates, lipids, free amino acids, vitamins, and terpenes (Lynn and Clevette-Radford, 1987).
The latex of leafy spurge is produced and stored in non-articulated laticifer cells which are present throughout the plant. Laticifer initials arise in the meristematic mass of the developing embryo. Each initial is capable of unlimited growth (Mahlberg and Sabharwal, 1968). The laticifer system has been suggested to serve as a nutritional reservoir, conductive system, water balance regulator, defense system from herbivores, and as a storage system for cellular byproducts. The presence of terpenes and alkaloids supports the idea that laticifers function as a storage and/or excretory system for secondary plant products (Biesboer and Mahlberg, 1978). Starch grains present in the laticifers are not utilized as an energy reserve but rather in wound closure (Biesboer and Mahlberg, 1981).

The latex of the genus *Euphorbia* may serve as a physical and chemical defensive mechanism. Chewing and piercing-sucking mouthparts of insects become clogged with latex when feeding on leafy spurge (Best et al., 1980). Diterpenes and triterpenes isolated from the latex are potential anti-herbivore compounds. The diterpenes, ingenol, 12-deoxy-phorbol, and their ester derivatives, are found in latex of many plants in the genus *Euphorbia* (Evans and Kinghorn, 1977). Latex containing ingenol and 12-deoxy-phorbol has been used as an insecticide, fish poison, arrow poison, and treatment for scabies and ringworm (Evans and Kinghorn, 1975). Therefore, the latex may discourage herbivores, except for those which have evolved adaptations for feeding on this plant (Best et al., 1980).

**ROOT RESERVES**

Leafy spurge and other perennial weeds store reserve carbohydrates and nitrogenous compounds in their roots. Carbohydrates are the major energy storage molecules in leafy spurge (Cyr and Bewley, 1990) and other perennial plants (Arny, 1932). In temperate species, excess photoassimilate is stored as nonstructural polysaccharides in underground storage tissue during summer and fall. These polysaccharides are hydrolyzed to soluble sugars while overwintering and used for maintenance respiration and as an energy source to fuel growth in the spring before leaves are capable of photosynthesis (Cyr and Bewley, 1989). Although carbohydrates are quantitatively the most important form of energy reserve, nitrogenous compounds may be as important qualitatively (Cyr and Bewley, 1989). Amino acids and soluble protein are cycled similar to sucrose and may be a critical storage currency (Cyr and Bewley, 1990).

Total nonstructural carbohydrate (TNC) is a measure of carbohydrate available for metabolism or translocation. Total nonstructural carbohydrate is made up of a soluble fraction, predominantly sucrose, and an insoluble fraction, starch (Lym and Messersmith, 1987). The seasonal pattern of root TNC content is variable. Lym and Messersmith (1987) reported on leafy spurge root TNC averaged over four growing seasons. They found that TNC was lowest in April, increased to a maximum in July, August, and September and then declined through October. This is in disagreement with what Arny (1932) found. Arny described the total readily available carbohydrate content of leafy spurge roots as being fairly high in April, decreasing in May, gradually increasing

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through October, and then declining in November. In studies conducted at SD-SU, TNC in both shallow roots (0 to 15-cm depth) and root crown followed the pattern described by Lym and Messersmith (Scholes, 1996).

Lym and Messersmith (1987) found a high correlation between TNC and temperature, but no correlation with precipitation patterns. Leafy spurge utilized soluble sugars when stressed by high temperatures and replaced those sugars during periods of cool temperatures. Mowing and smother treatments, lowered TNC concentrations in both crown and root tissues (Scholes, 1996) with crown tissue more affected by treatment.

Variations in root reserves of other perennial weeds such as Canada thistle (Cirsium arvense [L.] Scop.), perennial sowthistle (Sonchus arvensis [L.]), quackgrass (Elytrigia repens [L.] Nevski), and field bindweed (Convolvulus arvensis [L.]) have been studied. Root reserve patterns for these species are dissimilar. For example, Canada thistle root carbohydrate reserves decline from May through June or July and then increase through September (Tworkoski, 1992). The decline in root reserves appeared to be related to growth early in the season but in early fall photoassimilate movement in the phloem was basipetal, increasing root reserve storage.

Perennial sowthistle root carbohydrate levels follow the same general seasonal pattern as Canada thistle, with reserves lowest during flowering (Arny, 1932). Quackgrass TNC was lower than that of Canada thistle, perennial sowthistle, or leafy spurge, particularly during October and November (Arny, 1932). Quackgrass carbohydrate levels remained fairly constant between late April and early November.

Cyr and Bewley (1989) found seasonal variation in free amino acids, soluble protein, and nitrate plus nitrite levels in leafy spurge roots. Free amino acids, soluble protein, and nitrate + nitrite were lowest in August and September but increased rapidly by October because of remobilization during senescence. Abundance of individual amino acids changed throughout the year, indicating different roles in the nitrogen budget of leafy spurge. Weekly treatments of defoliation and decapitation of leafy spurge that began in August decreased soluble protein and free amino acids in leafy spurge roots by November and nitrate by December (Cyr and Bewley, 1990). These decreases may have been caused by remobilization of nitrogen from the root to meristem important for regeneration, i.e. adventitious root buds.

**CULTURAL CONTROL**

Cultural control of weeds is, strictly, the use of control practices on cultivated land. Derscheid et al. (1985) expanded this definition to include all non-chemical methods including grazing livestock. Sheep and goat grazing will be considered as biological control here. Intensive cultivation can be effective in eliminating leafy spurge stands. However, much of the land infested with leafy spurge is pasture or rangeland that cannot be cultivated. The use of competitive crops is another cultural control method but few crops can outcompete leafy spurge without the complementary use of cultivation or herbicides (Derscheid et al., 1960). Plastic smother and mowing are other potential cultural control methods.
Frazier (1943) investigated the effects of 7-day and 14-day intervals of cultivation on field bindweed root carbohydrate reserves. The longer cultivation interval depleted carbohydrate reserves more than the 7-day interval. The 14-day cultivation interval allowed new field bindweed shoots to emerge about 6 days after cultivation, and these shoots continued to draw on carbohydrate reserves for 8 days after emergence. The shoot emergence decreased root reserves without allowing replacement of photoassimilates.

Covering the soil surface with clear or black polyethylene for control of pathogens, nematodes, and weeds has been used as an alternative to chemical control methods. The method has been termed solarization or plastic mulch but will be referred to as plastic smother here. Plastic smother captures radiant heat energy from the sun that alters the microclimate in the soil rhizosphere (Al-Masoom et al., 1993), and causes soil temperatures to increase and nitrate leaching to decrease (Clarkson, 1960).

Plastic smother can reduce weed populations by decreasing the number of viable seeds or by killing seedlings and mature plants. Weed seed viability can be reduced by modifying soil temperature, moisture, carbon dioxide, oxygen, and ethylene with plastic smother (Egley, 1990). Moist heated soil is much more detrimental to seeds than dry heated soil. Egley (1990) found that dry soil maintained at 60°C for 7 days only slightly decreased seed survival. However, moist soil maintained at 60°C for 7 days increased seed mortality from 70 to 100%. Moist soil maintained at an elevated temperature can break mechanical (seed coat) seed dormancy. Those seeds not succumbing to the high temperature will be induced to germinate with the seedling likely to perish in the hot soil (Egley, 1990).

Plastic smother or solarization has been used most often in areas where the growing season is preceded by a hot, dry period such as in California, Israel (Horowitz et al., 1983), India (Kumar et al., 1993), Greece (Vizantinopoulos and Katranis, 1993), Jordan (Abu-Imaleh, 1991), and the United Arab Emirates (Al-Masoom et al., 1993). In these areas, plastic smother is typically used as a pre-plant treatment. Duration of the plastic smother treatment varies between 1 week to 2 months. Horowitz et al. (1983) studied duration of plastic smother and its effects on weed emergence after removal of the plastic. A treatment period of 2 weeks controlled most weed species for at least 1 year. A 6 week plastic smother treatment gave 100% control of common purslane 3 months after treatment (MAT), henbit 4 MAT, and field bindweed 2 MAT.

In contrast to the use of plastic smother as a pre-plant soil sterilization technique in agriculture, horticulturists use plastic as a mulch to smother weeds during crop growth or as a long-term weed suppression measure in landscaped areas (Martin et al., 1991). Crops such as tomato, basil, parsley, and rosemary can be grown through holes in the plastic that suppresses most weed growth. Additional advantages to this technique include an increase in soil temperature, conservation of moisture, reduction of nutrient leaching, reduction of soil compaction, and increased CO2 levels (Ricotta and Masiunas, 1991). Because elevated soil temperatures under plastic quickly decrease with depth (Horowitz et al., 1983), roots of crops grown through plastic can grow in warm soil without drying.
Black plastic reduced both leafy spurge stem density and biomass and flowering was prevented (Clay and Scholes, 1997). Two months after application, biomass was reduced by 66%. After 2 continuous years of treatment, virtually no leafy spurge was present (Clay and Scholes, 1997). The problem with this treatment is that all other vegetation under the plastic died also. When treatment was removed after one season, leafy spurge reinfested the areas rapidly, with biomass equal to control areas by early June of the second year and grass biomass less than 200% of the control (Clay and Scholes, 1997). Areas that are treated in this manner must be reseeded with competitive grass species such as "Bozoisky" Russian wild rye (Elymus junceusi Fisch.) or "Roden" western wheatgrass (Agropyron smithii Rydb.) (Christianson and Lym, 1984) in order to suppress reinfestation.

Mowing is a method used to prevent seed production or lower root reserves. By mowing at 14 day intervals the spurge plant uses stored carbohydrates to regenerate stems and leaves but does not regenerate the root reserves through photosynthesis (Derscheid et al., 1985). Removing the stem will release the root and shoot adventitious buds from apical dormancy. This will stimulate growth of lateral buds, possibly increasing stem density.

Peters and Lowance (1978) mowed western ironweed (Vernonia baldwinii) and gray goldenrod (Solidago nemoralis) multiple times as a means of control. Both plants are perennials with the ability to produce shoots from adventitious root buds. Initially the mowing treatment caused an increase in western ironweed density because of its ability to produce shoots from adventitious root buds. However, western ironweed shoot density was reduced 81% after 2 years of mowing 3 times per year.

Gray goldenrod stem density also was reduced by repeated mowing (Peters and Lowance 1978). Gray goldenrod stand density was reduced up to 85% after one year of 2 mowing treatments per year and up to 97% after two years of repeated mowing.

Mowing at two and four week intervals reduced leafy spurge biomass by > 95% after the first treatment (Clay and Scholes, 1997). After two years of treatment, virtually no leafy spurge was left in the mowed areas and plants that remained did not flower. When treatment was removed after the first year, leafy spurge recovered, however, grass biomass was 50 to 100% more than that of the control.

CHEMICAL CONTROL

The use of herbicides to suppress leafy spurge is currently the most widely used control method (Alley and Messersmith, 1985). Bakke (1937) discussed the application of sodium chlorate, sodium chlorate plus glue and sulfuric acid, sodium chlorate plus calcium chloride (Atlacid), creosote-kerosene, sulfuric acid, ammonium thiocyanate, and potassium chlorate on leafy spurge. The sodium chlorate plus glue and sulfuric acid was very effective (Bakke, 1937) but was expensive and an extreme fire hazard (Alley and Messersmith, 1985). The introduction of 2,4-D [2,4-dichlorophenoxy)acetic acid] in the 1940's and dicamba (3,6-dichloro-2-methoxybenzoic acid) and picloram (4-amino-3,5,6-
trichloro-2-pyridinecarboxylic acid) in the 1960's began the modern era of herbicide use. Today, picloram, dicamba, and 2,4-D are the most commonly used herbicides for leafy spurge control (Alley and Messersmith, 1985).

Picloram at 2.24 kg ha⁻¹ (2 lb acre⁻¹) is the most consistently effective herbicide treatment for leafy spurge (Alley and Messersmith, 1985). However, in a study investigating the economics of leafy spurge control with herbicides, Gylling and Arnold (1985) found that the 2.24 kg ha⁻¹ picloram rate was the most expensive of all treatments in the study, and the increased forage available with this treatment did not pay for the treatment. Lym and Messersmith (1985) concluded that an annual spring or fall application of 0.28 kg ha⁻¹ of picloram in combination with 1.12 kg ha⁻¹ of 2,4-D was the most economically effective treatment.

Derscheid et al. (1960) experimented with several combinations of 2,4-D and brome grass to reduce leafy spurge stands. In combination with the brome grass, the herbicide treatments reduced leafy spurge stands up to 52% the first year and 81% the second year. Stand reduction was assessed in May of the year following treatment. Alley and Messersmith (1985) summarized numerous weed control guides, bulletins, etc. that suggested 1.12 to 2.24 kg ha⁻¹ 2,4-D will control the aboveground portion of the leafy spurge plant and seedlings, and usually prevent seed production for the year of application. A heavier rate applied at least twice a year for several years was considered necessary to reduce density of established stands. Bybee (1979) reported that 2,4-D at 1.12 kg ha⁻¹ prevented seed production but had no effect on the leafy spurge stand the next year.

Splitting the 2,4-D application into 0.11 kg ha⁻¹ treatments applied every two weeks gave very good control of leafy spurge, much better than a single 1.12 kg ha⁻¹ spring application (Clay and Scholes, 1997). Effects of the split treatment were not evident until after the fourth application but by the end of the season, only a trace of leafy spurge was present in the plots. Grass biomass was 60% greater in these plots than the check in the first year and was 100% greater in the second season of treatment. Plots recovering from one year of treatment had 100 to 200% more grass than an untreated check.

### BIOLOGICAL CONTROL

Biological control of weeds is the use of natural enemies to reduce weed populations to levels below an economic threshold (Harris et al., 1985). Biological control is based upon the assumption that introduced pests attain high population levels by escaping a “balance of nature existing in its native habitat” (Wilson and Huffaker, 1976). The aim of biological control is to establish a balance between the plant and its natural enemies introduced as biocontrol agents in the habitat the pest is infesting. Successful establishment of biological weed control agents may reduce herbicide use and the amount of energy used for chemical, mechanical, or physical weed control.

In most cases, plants considered for biological control are perennials inhabiting relatively low value land (Andres et al., 1976) or ecologically sensitive areas such as riparian habitats or shelterbelts. In these areas, chemical or me-
Mechanical control methods are often unusable, uneconomical, or physically impossible.

While cattle avoid leafy spurge, goats and sheep are considered to be biological control agents of it. Johnston and Peake (1960) reported on the use of sheep to control leafy spurge more than 30 years ago. They found that five years of sheep grazing gave 98% control of leafy spurge. Since then, there have been conflicting reports on the attractiveness of leafy spurge to sheep. Landgraf et al. (1984) reported that sheep will consume up to 50% of their diet in leafy spurge. However, Kronberg and Walker (1993) reported that sheep did not consume leafy spurge because fermentation of leafy spurge in the rumen either did not detoxify the aversive compound of leafy spurge or created a flavor aversion by producing a chemical irritant. In contrast, sheep exposed to goat digesta of leafy spurge did not develop a flavor aversion.

Lambs can be trained to consume leafy spurge and introduction to the weed at an early age impacts later consumption (Walker et al., 1992). This early learning by lambs is important to being a selective grazer and, therefore, an effective biocontrol agent.

While references to grazing leafy spurge with goats are scarce, it is not an uncommon practice. Goats appear to accept leafy spurge as a food source more willingly than sheep. This may be explained by the finding that aversions encountered by cattle (Kronberg et al., 1993) and sheep while or after digesting leafy spurge are not encountered by goats (Kronberg and Walker, 1993).

Insect introductions have become a major weed biocontrol tactic in the United States. The insects may feed on the root system, foliage, vascular tissue, or flowers, all of which reduce the vigor or reproductive capacity of the plant. Insects that attack the plant where damage is most stressful to the plant are the most successful biocontrol agents.

Introduced biocontrol agents must meet certain criteria (Andres et al., 1976). The most important criterion is that the insect be host specific. Potential biocontrol insects are tested rigorously to ensure that they do not attack desirable plants that may be associated with the weed to be controlled (Andres et al., 1976). The bioagent must be adapted or adaptable to the environment that the introduced weed species is inhabiting. The introduced agent also must be able to locate the host plant and reproduce quickly enough to affect the given weed. Finally, the insect must be introduced free from its own parasites and diseases (Andres et al., 1976).

Leafy spurge is a good candidate for biological control because it is a perennial plant that often inhabits low value land. Several species of insects associated with the leafy spurge complex in Europe and Asia have been introduced as biological control agents in the United States and Canada. The spurge hawkmoth (Hyles euphorbiae L.), a defoliator, was released in Canada and then in the United States as the first biological control attempt on leafy spurge in 1965 (Harris, 1984). The hawkmoth is very susceptible to predation by several species of insects (Forwood and McCarty, 1983) and, therefore, was difficult to establish. In addition, a virus associated with this species has prevented an increase in the population (Spencer, 1994). Hyles euphorbiae has been estab-
lished in Ontario and at one site in Montana, but the populations are not prolific enough to be of any value in controlling the leafy spurge (Harris, 1984).

Two moths with root boring larvae, Chamaesphecia tentbradiniformis D. & S. and C. empiformis Esp., were released in the United States and Canada between 1970 and 1974. These moths never became established (Harris, 1984).

Oberea erythrocephala Schrank is a beetle whose larvae mine leafy spurge root and stem tissue. It was released in Canada (Harris, 1984), Montana, Oregon, and Wyoming between 1980 and 1984 (Rees et al., 1986). This long-horned beetle is well established in Montana and seems to prefer areas where leafy spurge stem diameter is 2.5 mm or greater (Spencer, 1994). The population growth of this beetle is very slow and took about 10 years to increase to damaging levels.

The leafy spurge gall fly [Spurgia esula (Bremi)] has been successfully established in the United States and Canada (Julien, 1987). The gall fly reduces seed production through the formation of galls on the terminal ends of shoots rather than reducing the stem density of the spurge. Gall fly establishment thus far has been limited to sheltered areas, specifically tree belts. Gall flies may complete up to five life cycles during a normal season (Plant Protection and Quarantine, 1989). The gall fly could be important in reducing seed production while other biocontrol agents are being established to reduce the density of leafy spurge.

Current efforts are focused on Aphthona flea beetles, which have shown some signs of being successful biological control agents. Six species of flea beetles [A. abdominalis Duftschmid, A. cyparissiae (Koch), A. czwalinae Weise, A. flava Guill., and A. nigriscutis Foudr.] have been released as biological control agents for leafy spurge in the United States. Sommer and Maw (1982) reported that the apex and ventral groove of the aedeagus, two characteristics used to distinguish between Aphthona spp. are not reliable for positive identification. McDaniel et al. (1992) demonstrated that other aedeagus (male reproductive structure) characteristics could be used to reliably separate A. cyparissiae, A. flava, A. nigriscutis, and a native flea beetle Glyiptina atriventris Horn.

Aphthona cyparissiae was first released as a biocontrol agent in North America in 1982. It was originally collected from Austria, Hungary, and Switzerland. Aphthona czwalinae was first released in 1985, with original stock coming from Austria and Hungary. Aphthona flava was collected in Hungary and Italy and released in 1982. In 1983 Aphthona nigriscutis was released after being collected in Hungary (Julien, 1987).

The five univoltine flea beetles (A. cyparissiae, A. czwalinae, A. flava, A. lacertosa, and A. nigriscutis) have similar life cycles. In Europe, males and females of these Aphthona beetles emerge simultaneously in June in an approximate 1:1 ratio. Oviposition begins one week after emergence and continues for up to 14 weeks. Under laboratory conditions at 20°C eggs hatched at 16.9 ± 1.8 days (A. cyparissiae) and 18.6 ± 1.4 days (A. flava). The larvae progress through 3 instars. Larvae feed into the fall and form a cell for overwintering. Aphthona cyparissiae consistently survived a temperature of -7.2°C and A. nigriscutis consistently survived down to -5.5°C. Two A. cyparissiae larvae
survived down to -13.0º C, indicating the ability to supercool. Under laboratory conditions, pharate pupal development took between 28 and 57 days. Pupal duration lasted another 20 days (Sommer and Maw, 1982).

Univoltine flea beetles attack leafy spurge in two ways. The main impact is from larvae mining the roots, although adults feed on foliage. Root mining by the first instar larvae tends to be on the new filamentous roots, and as the larvae progress through the second and third instars they feed on older, perennial roots (Sommer and Maw, 1982). Root feeding by *Aphthona* spp. beetles reduces water and nutrient uptake by destroying the vascular tissue and provides an entrance for plant pathogens. The root feeding also may reduce carbohydrate reserves by isolating root fragments (Maw, 1981).

The four species of *Aphthona* released to date are reported to have different habitat preferences. *Aphthona nigriscutis* prefers dry, coarse-soiled sites that occur on knolls or south-facing slopes. *Aphthona cyparissiae* prefers open, mesic environments, such as in swales, whereas *A. flava* prefers mesic, shaded sites. *Aphthona czwalinae* establishes best in moist sites that are open or shaded (Plant Protection and Quarantine, 1989). Preliminary indications are that *A. lacertosa* survives best in habitats where grass overtops leafy spurge. The different habitat preferences of these flea beetles allows them to attack leafy spurge in the various environmental habitats.

A multivoltine species of flea beetle, *A. abdominalis* Duftschmid, was screened and approved for release in the United States in 1993 (Fornasari, 1993). *Aphthona abdominalis* larvae feed on roots, adventitious buds, and underground shoots. Adults feed on stems and leaves of leafy spurge. Unlike the species of *Aphthona* flea beetle previously discussed, *A. abdominalis* overwinters as an adult and could potentially produce four generations per year. The distribution of *A. abdominalis* between Poland and northern Iran (Fornasari, 1993) suggests that it could overwinter throughout the range of leafy spurge in North America, although it may produce less than 4 generations per year in the north. Because of its potential in producing multiple generations per year and the feeding damage it causes to leafy spurge, this flea beetle has great potential as a biological control agent for leafy spurge.

**SUMMARY**

Leafy spurge is a perennial, pernicious weed that primarily infests pasture and rangeland habitats. Control is expensive, and because of it’s spreading root system with adventitious buds, must be treated annually. Techniques that stress the plant throughout the growing season appear to give better control for a longer period of time than single treatments. Research into control techniques using insects and bacteria may provide the key to successful leafy spurge management in the future.
LITERATURE CITED


Sommer, G. and E. Maw. 1982. Aphthona cyparissiae (Koch) and A. flava (Guill.) (Coleoptera:Chrysomelidae): Two candidates for the biological control of cypress and leafy spurge in North America. CIBC Report. 60 pp.


