Euphorbia esula

INTRODUCTORY

Leafy spurge infestation in Montana.
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AUTHORSHIP AND CITATION:
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FEIS ABBREVIATION:
EUPESU

NRCS PLANT CODE [221]:
EUES
EUESE
EUESU

COMMON NAMES:

leafy spurge
Wolf's milk

TAXONOMY:
The scientific name of leafy spurge is *Euphorbia esula* subg. *Esula* L. (Euphorbiaceae) [43,59,90,156].

Kartesz [90] recognizes 3 leafy spurge varieties: leafy spurge (*Euphorbia esula* var. *esula*), Oriental leafy spurge (*E. esula* var. *orientalis*), and Russian leafy spurge (*E. esula* var. *uralensis*). Plants Database [221] recognizes only 2 varieties: leafy spurge and Russian leafy spurge. However, after analyzing 26 morphological characters for 600 *Euphorbia* species within the *Esula* subgenus, Crompton and others [43] concluded that in North America, leafy spurge is a single, variable species and has hybridized only with cypress spurge (*E. cyparissias*). Considerable taxonomic confusion surrounds leafy spurge varieties, subspecies, and hybrids (see the Synonyms section below). Likely multiple introductions of leafy spurge into North America resulted in a complex of variable genotypes [115].

Hybrids: Only the tetraploid cypress spurge type is known to hybridize with leafy spurge [148,167], resulting in the hybrid, *Euphorbia* × *pseudoesula* Schur. [43,147,148,174]. In Canada, *Euphorbia* × *pseudoesula* has been collected from British Columbia, Saskatchewan, and Ontario [207], but hybrids are possible anywhere leafy spurge and the tetraploid cypress spurge type occur together.

SYNONYMS:
for ***Euphorbia esula* var. *esula*:**
Euphorbia intercedens Podp. [42,90,221]
Euphorbia podperae Croizat [221]
Euphorbia × *pseudovirgata* (Schur) Soó [52,61]
Galarhoeus esula (L.) Rydb. [90,221]
Tithymalus esula (L.) Hill or Scopoli [90,221,232,233]

for ***Euphorbia esula* var. *uralensis*:**
Euphorbia esula var. *orientalis* Boiss. [221]
Euphorbia esula ssp. *tommasiniana* (Bertol.) Kuzmanov [42,174]
Euphorbia uralensis Fisch. ex Link [42,174]
Euphorbia virgata Waldst. & Kit., non Desf. [42,52,61,90,221]
Tithymalus uralensis (Fisch. ex Link) Prokhanov [90,221,232,233]

LIFE FORM:
Forb

DISTRIBUTION AND OCCURRENCE

SPECIES: Euphorbia esula

- GENERAL DISTRIBUTION
- HABITAT TYPES AND PLANT COMMUNITIES

GENERAL DISTRIBUTION:
Leafy spurge is native to Eurasia but occurs as a nonnative species nearly throughout western North America and the central two-thirds of eastern North America [59,221]. At the edges of this range, leafy spurge is less common. In western Canada, leafy spurge is known as far north as Yukon. Leafy spurge is rare along the Pacific Northwest Coast [166] and is generally restricted to the northern regions of California, Nevada, Arizona, and New Mexico [3,21,78,91,131]. In the Great Plains, leafy spurge is much more common in the northern 75% than the southern 25%

[61], and it is rare along the Atlantic Coast [49].

Leafy spurge is most widespread and invasive in the US states of Oregon, Idaho, Montana, Wyoming, Colorado, North Dakota, South Dakota, Nebraska, Minnesota, and Wisconsin [17,118]. By 1975, leafy spurge populations were largest and most extensive in the Great Plains region and occurred in 80 counties in Minnesota, 54 in Montana, 54 in Nebraska, 52 in North Dakota, and 49 in South Dakota [50]. As of 1979, leafy spurge occupied 2.5 million acres (1 million ha) in North America, including 800,000 acres (320,000 ha) in Minnesota, 600,000 acres (240,000 ha) in North Dakota, and 543,000 acres (220,000 ha) in Montana [154]. By 2000, 1.2 million acres (490,000 ha) of rangelands in North Dakota were infested by leafy spurge (Lym and others 2000 cited in [46]). As of 2005, leafy spurge occupied an estimated 4.6 million acres (1.9 million ha) in the United States, of which about half or more was rangeland in the northern Great Plains [46,118].

The Russian leafy spurge variety that is recognized by some [90,221] is found in scattered locations from Saskatchewan to Colorado and Kansas and from Michigan to Pennsylvania and Connecticut. However, only the typical variety is reported in the Northeast by Magee and Ahles [129]. Leafy spurge and Russian leafy spurge distributions are available from the Plants Database website.

Introduction to North America: There were likely many separate introductions of leafy spurge to North America [52,200]. In a review, Dunn [51] suggests at least 4 possible early introductions of leafy spurge in North America. The first US leafy spurge collection was made in 1827 from Newbury, Massachusetts, where leafy spurge was thought to originate from a ballast dump. The first Canadian leafy spurge collection was made in 1899 from Huron County, Ontario; the species was likely brought by Russian immigrants in contaminated spelt from Germany [19,51]. Early spread of leafy spurge in North America was attributed to the planting and cultivation of contaminated smooth brome (*Bromus inermis*) and cereal seed from within and outside North America [6,51,200]. Royer and Dickinson [191] suggest that leafy spurge in Massachusetts came from the Caucasus region of western Asia, and leafy spurge found in Minnesota in 1890 came from Russia. When researchers compared the DNA from leafy spurge plants collected from Nebraska, Montana, Russia, Italy, and Austria, they found the DNA in plants from Nebraska, Montana, and Russia to be most similar [153]. In another DNA study, researchers found a high degree of genetic variability among 123 leafy spurge plants collected from Colorado, North Dakota, South Dakota, and Nebraska, which suggested multiple North American introductions or a high degree of variability for leafy spurge in its native range [190].

Perhaps because of multiple introductions and the cultivation of contaminated crops, leafy spurge was widespread in the northern United States and southern Canada by the early 1900s. Leafy spurge occurred in Ontario by 1889 [191] and in Iowa by 1899 [6]. As of 1900, it was described as "naturalized" in parts of the northeastern United States [156]. Leafy spurge was also reported in Oregon and Washington by 1900 and in Idaho in the early 1900s [34]. Although leafy spurge was found in 2 Michigan counties before 1900, the majority of collections occurred after 1930 [226]. Leafy spurge was quite common throughout New York by 1924 [151], and occurred in Nova Scotia by 1928 [189] and in British Columbia by 1939 [191]. In Arizona, however, leafy spurge was first collected from Coconino County in 1970 [3].

Local distribution changes: Several studies report dense populations as well as rapid spread of leafy spurge in North America. Populations with densities of 1,000 stems/yard² are not uncommon [21]. By 1962 in Canada, 35,000 to 40,000 acres (14,000-16,000 ha) were occupied by leafy spurge. In a Saskatchewan municipality, the acreage infested with leafy spurge more than doubled in 3 years despite control efforts [199]. In North Dakota, the number of acres with leafy spurge doubled in the 9-year period from 1973 to 1982 [17]. The annual spread rate for leafy spurge from 1909 to 2002 in North Dakota was about 16% [118]. In Montana's Lolo National Forest, the estimated 10-year spread rate was reported as 100% in an Environmental Impact Statement draft published in 1989 [219]. A 2005 Weed Science Society of America publication reported that the "historic" annual spread rate of leafy spurge in the United States ranged from 12% to 16%. The time frame used to estimate this rate was not reported [48].

HABITAT TYPES AND PLANT COMMUNITIES:
Grasslands, riparian areas, shrublands, and savannas are common habitat for leafy spurge in its native and nonnative ranges. In Europe, leafy spurge is often associated with sandy sites, is especially common in dry meadows, and often occurs along roads and stream banks (review by [200]).

In North America, leafy spurge occupies a variety of habitat types and plant communities but "exhibits maximum vigor" in ungrazed, native grasslands [199]. Researchers reported that in Saskatchewan leafy spurge occurs "in almost every conceivable habitat, with the exception of boreal forest" (reviews by [199,200]). Throughout Canada's southern provinces, leafy spurge is most common in prairies, savannas, and open woodlands [235]. In Massachusetts, leafy spurge occurs in grasslands and coastal habitats [132], and in Wisconsin, it "flourishes in open-grown oak woods" (reviews by [199,200]).

Numerous vegetation types are described for leafy spurge habitats in the western and Great Plains regions of the United States. Leafy spurge is especially common in prairies, meadows, and woodlands [17,80,213]. In eastern Oregon's John Day River Basin, leafy spurge occurs in Lewis' mockorange-mallow ninebark-oceanspray (*Philadelphus lewisii*-*Physocarpus malvaceus*-*Holodiscus discolor*) and big sagebrush/western juniper/cheatgrass-bluebunch wheatgrass (*Artemisia tridentata*/*Juniperus occidentalis*/*Bromus tectorum*-*Pseudoroegneria spicata*) vegetation types along shallow streams but achieves its greatest importance value in big sagebrush communities [130]. Throughout sagebrush ecosystems in the Intermountain West, leafy spurge is described as "highly invasive and competitive" [172]. After stream surveys, researchers estimated that leafy spurge occupied 3.5% of perennial stream length in the western United States and 20.2% of perennial stream length in the Great Plains. In North Dakota and South Dakota, leafy spurge occupied 59% and 13.8% of perennial stream length, respectively [187]. Leafy spurge occurred on Montana's Pine Butte Swamp Preserve; it formed near monocultures in some grasslands, riparian areas, and limber pine savannas [177]. In North Dakota's Theodore Roosevelt National Park, researchers identified 11 plant associations that were "particularly susceptible" to invasion by leafy spurge including floodplain, grassland, shrubland, and woodland communities. In silver sagebrush (*A. cana*), creeping juniper (*J. horizontalis*), and prairie sandreed (*Calamovilfa longifolia*) associations, species richness was significantly lower in leafy spurge infested than noninfested plots (P<0.05) [29].

BOTANICAL AND ECOLOGICAL CHARACTERISTICS

SPECIES: Euphorbia esula

- GENERAL BOTANICAL CHARACTERISTICS
- SEASONAL DEVELOPMENT
- REGENERATION PROCESSES
- SITE CHARACTERISTICS
- SUCCESSIONAL STATUS

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GENERAL BOTANICAL CHARACTERISTICS:

- **Botanical description**
- **Raunkiaer life form**

Botanical description: This description covers characteristics that may be relevant to fire ecology and is not meant for identification. Keys for identification are available (e.g., [59,61,81,226]).

Aboveground description: Leafy spurge is an erect, perennial forb that grows 8 to 35 inches (20-90 cm) tall [78,81,91]. Because of prolific vegetative growth, leafy spurge often grows in rather thick clumps [13]. Although herbaceous, stems have a woody texture and when mature, are nearly shrubby [6]. Damaged stems ooze a milky fluid [129]. Stems are simple, but near the inflorescences, they have umbrella-like branching and dense leaves [61,99,131]. Linear stem leaves are 2 to 6 inches (5-15 cm) long and about 4 to 8 times as long as they are wide [44,78,91,152]. At the stem bases, leaves are reduced [226]. Leaves associated with the inflorescences are heart-shaped [99,222]. Inflorescences are comprised of a single pistillate and 12 to 25 staminate flowers. Flowers are greatly reduced and lack both sepals and petals [61,81,234]. Leafy spurge generally produces a very small, 3-chambered capsule that produces 2 to 2.5 mm seeds [78,234]. Four- and five-chambered capsules have been observed, although rarely [199,200]. When mature, capsules "explode" to eject seeds [13]. For more about this, see the Seed dispersal section below.

Look-alikes and hybrids: Leafy spurge is similar in appearance to cypress spurge. In general, leafy spurge is larger and produces fewer and larger leaves than cypress spurge. *Euphorbia* × *pseudoesula* plant height, leaf size, and leaf abundance are generally intermediate to what is characteristic of the parents, although hybrids more closely resemble leafy spurge than cypress spurge. For more on identifying and distinguishing cypress spurge, leafy spurge, and *Euphorbia* × *pseudoesula* see these references: [15,147,148,191,213,222].

Belowground description:

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Leafy spurge produces a persistent, prolific, and often deep and massive root system [44,49]. Although typically described as persistent, the life span of leafy spurge's perennial root system was not reported in the literature available as of 2010.

Substantial vegetative growth and clonal spread occur through root sprouting in leafy spurge [152]. Although some refer to the sprouting roots as rhizomes [61,118,234], after years of studying the anatomy and morphology of leafy spurge in the laboratory, Raju [175] reported that "morphologically specialized structures such as runners or rhizomes (we)re not observed". In an earlier publication, Raju and others [176] acknowledged that "the phenomenon of shoot-bud production by roots (wa)s interesting...as a fundamental problem in morphogenesis".

Several excavation studies show that the leafy spurge root system is dense and deep. The root systems of mature leafy spurge plants excavated from clay soils near Fargo, North Dakota, had numerous coarse and fine roots that occupied a large volume of soil. Coarse roots were woody, tough, and produced numerous buds. Researchers described "extreme development" of fine, white roots in the upper 2 feet (0.6 m) of soil. Roots within the top 1 foot (0.3 m) of soil were as much as 0.5 inch (1.3 cm) in diameter. Large horizontal roots occurred as deep as 20 inches (50 cm) and produced shoots 1 to 3.5 feet (0.3- 1.1 m) away from the parent plant. Vertical roots reached the water table, which was 8 feet (2.4 m) below the soil surface. In dense leafy spurge stands, "the mass of roots in the soil (wa)s enormous" [73]. Plants excavated from constantly moist soils in a field in Iowa had 8 vertical roots that reached over 12 feet (3.7 m) deep. The deepest root was 15 feet 8 inches (4.8 m). Based on root aging estimates, the excavated plant was 10 years old [6]. Leafy spurge roots extended more than 10 feet (3 m) deep in sandy loam soils near Saskatoon, Saskatchewan. Fragments from roots collected at 9 feet deep (2.7 m) produced shoots when planted [176]. For a description of seedling roots, see Seedling establishment.

Soil texture and fertility can affect growth and distribution of leafy spurge roots. In Saskatchewan, soil texture affected root distribution, and past land use affected total root weight of leafy spurge. In fine soils, leafy spurge roots were thick in the top 6 inches (15 cm) of soil. In coarse soils, roots were thick at soil depths below 30 inches (76 cm). Root weight in undisturbed native grasslands was about twice that of recently cultivated areas [199]. In a greenhouse experiment, leafy spurge roots grew downward about twice as fast in sandy soil as in clay soil. Roots in clay soil had greater branching than those in sandy soil [73]. Controlled outdoor experiments showed that high levels of soil nitrogen can reduce the biomass of leafy spurge roots and lead to greater root concentrations near the top of the soil profile [188].

Raunkiaer [179] **life form:**
Hemicryptophyte

SEASONAL DEVELOPMENT:

General phenology: Several studies from the northern Great Plains region of North America have reported details regarding leafy spurge phenology. Seedlings typically emerge in the spring (see Emergence timing for details). In

Saskatchewan, leafy spurge shoots emerge from established plants from mid-April to early May and flowers appear by early to late May, sometimes within a week of emergence [199]. Flowering and seed development are continuous, generally occurring from late April to mid-August; sometimes they occur into late October or November. Leafy spurge disperses most seed by mid-September [199,200]. Flowering and seed production can be delayed if leafy spurge plants are disturbed [13]. In northwestern Iowa, leafy spurge is one of the first weeds to emerge in the spring. By mid-April shoots may be 6 inches (15 cm) tall. Plants are in full bloom by the first of June and produce seed from June until the first freeze. The same leafy spurge stem can produce seed over a period several weeks long period and also produce more than 1 seed crop/season [6].

Regional flowering dates: Leafy spurge generally begins to flower in May. Flowers are later, typically in June, in northern California [152], northern Nevada [91], and in Fargo, North Dakota [209]. Flowering occurs only until June in California [152] and Nevada [91] but extends into August in the rest of the Intermountain West [44]. Flowering occurs from May to September in northern New Mexico [131], the Great Plains [12,61], and West Virginia [212]. Flowers may occur on leafy spurge until October in the northeastern United States [129].

When grown and monitored for 2 years in field plots in Saskatchewan or Ontario, the flowering period of artificially produced *Euphorbia* × *pseudoesula* hybrids was longer than that of either parent in the same area. Hybrids flowered first from early May to late June and generally produced flowers again that lasted through late September. A second flowering flush was not observed for leafy spurge or cypress spurge [147].

Root carbohydrate storage: Several studies report fluctuations in leafy spurge's root carbohydrate stores, which are usually lowest in spring. Study findings may be useful in determining optimal timing of control measures. Total nonstructural carbohydrates (TNC) stored in the roots of leafy spurge in Fargo, North Dakota, reached a maximum in mid-summer and early fall and were lowest in early spring [120]. In south-central Nebraska, researchers found that TNC began accumulating in leafy spurge roots after flowering in mid-July. New root buds did not develop until late August or early September, suggesting that translocation of carbohydrates was greatest from late September to the first freeze, which researchers suggested may represent an effective time for herbicide treatments [206]. For leafy spurge plants in Washington County, Minnesota, readily available carbohydrates and total carbohydrate stores were low at the flowering stage (mid-May) and again in early July [4]. Root carbohydrate stores for leafy spurge plants in a field near Guelph, Ontario, were not substantially affected by defoliation [45]. While the above studies may be useful to leafy spurge control and management, the substantial regenerative capacity of a very small root piece (see Vegetative regeneration) suggests that leafy spurge regrowth may not be limited by low amounts of root carbohydrate stores.

REGENERATION PROCESSES:
Leafy spurge reproduces sexually by seed and regenerates asexually by root sprouting. Reproduction and regeneration topics are covered in more detail below.

- **Pollination and breeding system**
- **Seed production**
- **Seed dispersal**
- **Seed banking**
- **Germination**
- **Seedling establishment and plant growth**
- **Vegetative regeneration**

Pollination and breeding system: Leafy spurge produces unisexual flowers on typically monoecious plants [99,234]. Flowers are primarily pollinated by insects [6,200]. Although researchers found a leafy spurge population in Saskatchewan that produced only female flowers, dioecious plants are rare [199].

Leafy spurge is protogynous, and self-fertilization is limited. Because leafy spurge produces sticky pollen, wind pollination of flowers is unlikely [6]. While wind is not important to pollen dispersal, it may cause flower contact. When flowering leafy spurge shoots were located near a fan but protected from insects, a few capsules developed

[199].

Insects are important to pollination of leafy spurge flowers, and typically cross-pollination results in greater seed production than self-pollination. Seed was rarely produced on leafy spurge stems protected from insects, but on unprotected stems seed production was normal. The low levels of seed production on protected stems were likely the result of incomplete protection, since the researcher observed an ant inside the protection screen. In a greenhouse study, leafy spurge failed to produce seed until the insect-free area was contaminated by a house fly [200]. In artificial pollination experiments, 28% of flowers produced seed when female flowers were pollinated by male flowers from the same inflorescence; 41.3% of flowers produced seed when female flowers were pollinated by male flowers from the same stem; and 56.4% of flowers produced seed when female flowers were pollinated by male flowers from different plants [199,200]. During experiments on leafy spurge in a prairie near Grand Forks, North Dakota, 63% of female flowers pollinated by male flowers at least 82 feet (25 m) away produced seed, and 29% of self-fertilized female flowers produced seed [196].

Many insect visitors have been observed on leafy spurge flowers. During weekly growing-season collections made in Jameson, Saskatchewan, researchers identified 196 insect species associated with leafy spurge patches. The insects represented 13 orders and 84 families. There was little damage to leafy spurge plants, suggesting that most insects were utilizing leafy spurge pollen and nectar sources (Maw unpublished data cited in [15]). The soldier beetle (*Chauliognathus pennsylvanicus*) pollinated leafy spurge flowers in a field in Iowa [6]. Selleck [200] observed ants, bees, flies, and mosquitoes feeding on leafy spurge nectar in Saskatchewan.

Seed production: Leafy spurge can produce abundant seed, but first-year plants do not produce seed [199]. Mature seeds develop about 30 days after pollination [21].

Several studies report high levels of seed production by leafy spurge. An "average-sized", well developed leafy spurge plant growing with little competition in North Dakota produced 140 seeds/main stem at a time when maximum seed production was likely [210]. Average seed rain in the center of leafy spurge patches in Saskatchewan was 2,500 seeds/m². Seed rain ranged from 790 to 8,020 seeds/m² (Thomas unpublished data cited in [15]).

Leafy spurge seed yield can be affected by habitat and climate. In an Idaho fescue-bluebunch wheatgrass vegetation type in Gallatin County, Montana, leafy spurge seed production was much greater in cool, wet springs than in warm, dry springs [160]. In Saskatchewan, leafy spurge seed production was greatest (252 seeds/stem) in a native grassland and lowest (196 seeds/stem) in an old field seeded to crested wheatgrass (*Agropyron cristatum*). A maximum of 426 seeds/leafy spurge stem was recorded in a north-facing grassland [199,200]. At one site in Saskatchewan, leafy spurge seed production was rare over an 8-year period, and no seedlings emerged from collected soil samples. Additional observations revealed no male flowers. When plants from this site were planted near another leafy spurge population with male flowers, seed was produced. Seed yield in various leafy spurge stands in Saskatchewan ranged from 24 to 3,400 lbs/acre [199].

Seed dispersal: Seeds are forcibly ejected up to 15 feet (4.5 m) from mature, dry leafy spurge capsules [198]. Even longer distance seed dispersal is possible by animals [98,163,165,227] and water [37,199].

Capsule ejection: Researchers conducted indoor and outdoor experiments to determine normal and maximum seed ejection distances from leafy spurge capsules. Indoors the maximum ejection distance was 13.3 feet (4 m), and many seeds were 9 feet (2.7 m) from the stems. Outdoors the maximum ejection distance was 13.5 feet (4.1 m), which was also the maximum radius of the seed-catching canvas, so longer distance dispersal may have occurred. Just 1 seed fell within 1 foot (0.3 m) of the fruiting stalks. Researchers found no relationships between ejection distance and temperature, humidity, or sunlight levels [73]. While weather conditions may not affect ejection distance, they may affect ejection potential. In Saskatchewan, capsules did not explode on cloudy days but did eject seeds after 0.5 hour of sunshine. The researcher concluded that high temperatures and low humidity trigger eruption of leafy spurge capsules [200].

Animals: Domestic grazers, deer, game birds, and ants disperse leafy spurge seed. When leafy spurge seeds were fed to domestic sheep and goats, 14% of seeds passed by sheep were viable and 2% germinated; 31% of seeds passed by goats were viable and 16% germinated. Sheep passed all seeds in 9 days, and goats passed all seeds in 5 days [98]. In another study, sheep passed more mature than immature leafy spurge seeds, and the viability of recovered seed increased with seed maturity (0% for seeds in the soft dough stage, 41.4% in the hard dough stage, and 81.3% for mature seeeds) [161]. In a leafy spurge-infested rangeland in Gallatin County, Montana, sheep excreted 144 leafy spurge seeds/day at a time of peak seed production. Of the excreted seeds, 0 to 17 seeds/day were viable. Each shorn fleece averaged 38.7 leafy spurge seeds, but researchers doubted seeds in the fleece would be dispersed before being sheared or processed [163].

White-tailed deer, wild turkeys, sharp-tailed grouse, mourning doves, and ants are potential dispersers of leafy spurge seed. In northeastern Montana and western North Dakota, 1 leafy spurge seed germinated from collected deer feces. During feeding trials, however, the total viability of leafy spurge seeds passed by white-tailed deer ranged from 10.5% to 20.4%. Seeds were passed for 4 days, and viability was greatest for seeds passed 2 days after ingestion. No leafy spurge seedlings emerged from wild turkey feces collected from the same area, but in feeding trials, up to 53.8% of passed seeds were viable. In sharp-tailed grouse feeding trials, 2% to 25% of passed seeds were viable. For both wild turkeys and sharp-tailed grouse, only those seeds passed the first day after ingestion were viable [227]. From a sharp-tailed grouse dropping collected in North Dakota, 2 leafy spurge seedlings emerged [155]. Some leafy spurge seed collected from mourning dove crops germinated, but seeds from the digestive tract did not. Likely the only chance for dispersal would occur when parents regurgitate food for their young [6]. However, in north-central North Dakota, intact leafy spurge seeds were recovered from the feces of nestling mourning doves at 10 of 12 nests sites. Of the 110 recovered seeds, 25 germinated. Adult mourning doves did not pass intact seeds, suggesting that dispersal potential decreases with dove maturity [20].

Leafy spurge seeds have elaiosomes, which aid in dispersal by some ants. A study conducted in a big sagebrush-mixed-grassland in Park County, Montana, suggests that western thatching ants (*Formica obscuripes*) disperse leafy spurge seed. Ants removed 65% of seeds with elaiosomes and only 29% of seeds without elaiosomes. Level of seed removal was not significantly different between areas with high or low leafy spurge densities, but significantly fewer seeds were removed when caches were placed 330 feet (100 m) away from leafy spurge plants ($P<0.05$). The fate of seeds taken to the nests is unknown, but other ant species are known to discard seeds from their nests following removal of the elaiosome. Leafy spurge plants were often found on or near ant nests [165]. In Saskatchewan, boreal formicine ants (*Lasius* spp.) did not feed on the elaiosomes of leafy spurge seeds and did not store seeds in their burrows [199].

Water: Leafy spurge seeds can float in water [6] and survive underwater storage [37]. After 5 years of underwater storage in a canal in Prosser, Washington, a very small proportion of leafy spurge seeds germinated, but 90% of seeds remained firm [37]. Leafy spurge is often found along waterways, and sporadic populations often occur downstream from established stands. In southern Saskatchewan, leafy spurge populations often followed the contours of shallow basins that drained away surface water. Infestations followed some drainages for 600 feet (180 m) [199]. In the southern Rocky Mountains of Colorado, leafy spurge was absent from riparian areas downstream of dams [142].

Seed banking: Few studies specifically addressed the maximum longevity of the leafy spurge seed bank. Of the seed bank studies available, very few reported leafy spurge germination after more than 5 years in the soil. During field and laboratory studies conducted at the University of Saskatchewan, Selleck [198,200] found that some leafy spurge seeds germinated after 5 years in soil, but 99% of germination occurred in the first 2 years of burial. Seeds stored in metal containers at room temperature were still viable after 13 years [198,200].

Increased depth of burial may result in increased retention of viability in the leafy spurge seed bank. In Saskatchewan, leafy spurge seeds buried in mesh bags in fine sandy loam at 1-inch (2.5 cm), 2-inch (5 cm), 4-inch (10 cm), and 8-inch (20 cm) depths for 3 years had 12%, 18%, 43%, and 64% viability, respectively (Banting unpublished data cited in [15]). In a field study in Iowa, 61% and 68% of leafy spurge seeds germinated after 4 years of burial at 4 to 6 inches (10-15 cm) and 16 to 18 inches (40-46 cm) deep, respectively [27].

In Saskatchewan, the leafy spurge seed bank was depleted to 15 germinable seeds/m² after 8 years of continuous domestic sheep grazing. Seed bank density remained high (>4,800 germinable seeds/m²) on control sites and on sites treated with an herbicide 1 to 3 years earlier (<3,500 germinable seeds/m²) [22].

Germination: Seed dormancy mechanisms or controls are contained within the leafy spurge seed coat and are typically overcome by warm, moist conditions [56]. In the field, most leafy spurge seed germinates after several days at temperatures of 79 to 82 °F (26-28 °C) [199]. Average germination of seed collected from 4 locations in Saskatchewan ranged from 4% to 38% in the laboratory. Germination of seeds from the same site was similar in different years, suggesting a genetic difference in dormancy between sites [199]. In controlled studies, 48-hour freezing/thawing cycles slightly increased leafy spurge germination, and 48-hour wetting/drying cycles slightly decreased germination. Prolonged darkness promoted germination but scarification did not [198,200].

Timing: During field studies conducted near the University of Saskatchewan, maximum germination of leafy spurge seed occurred when seeds were 1 year old. Nearly all seeds germinated in May and June, although some germination continued through September [198,200]. When freshly ripe leafy spurge seeds were sown outdoors in the summer in North Dakota, 50% germinated the following spring [73], suggesting that summer temperatures may have been too hot for germination of a proportion of the seed.

Seed burial: In the laboratory, leafy spurge germination at 70 to 100 °F (20-40 °C) was often greater in dark than light conditions [199], suggesting that buried seeds may germinate better than seeds on the soil surface. In field studies, leafy spurge seedlings emerged from seeds just below soil surface and up to 2 inches (6 cm) deep. Germination was greatest at the 0.5-inch (1.2 cm) and 2-inch (5 cm) depths [176,198,200]. The greatest depth tested was 6 inches (15 cm) [198,200].

Temperature: Germination of leafy spurge seed is best at alternating, yet moderate temperatures. In laboratory studies, maximum leafy spurge germination occurred at alternating temperatures where the low was 68 °F (20 °C) and the high was 86 to 95 °F (30-35 °C) [27,198,200]. In other controlled studies, leafy spurge failed to germinate at temperatures at or below 37 °F (3 °C), but germination increased with increasing temperatures. At 82 to 88 °F (28-31 °C), germination was 43% on moist paper and 24% in moist soil [6].

Moisture: After 14 days in water, 13% of leafy spurge seeds germinated. Seeds on moist paper germinated better than those in water [198,199,200].

Soil texture: Leafy spurge seeds typically germinate better in clay than in coarser textured soils [198,200]. When the germination of leafy spurge seeds from several sites was compared in soils from the collection site and in uniform silty clay loams, germination was better in soils from the collection area ($P<0.01$), suggesting some degree of site adaptation. When seeds from a single source were tested, percent germination was greater in clays than in coarser soils [199]. In North Dakota's Little Missouri National Grasslands, leafy spurge emergence averaged 4.9% from soils collected from the floodplain and 3.8% from soils collected from upland sites [240].

Seedling establishment and plant growth: Most leafy spurge seedlings emerge early in the spring, although sporadic emergence can occur throughout the growing season (Thomas unpublished data cited in [15]). Soil texture, soil fertility, soil disturbances, and the presence of competing vegetation can affect leafy spurge seedling establishment, growth, and survival.

Emergence timing: Emergence of leafy spurge seedlings in the spring often follows heavy precipitation (Thomas unpublished data cited in [15]). Emergence can occur when temperatures are near freezing [17]. Although spring emergence is most common, in a field in Iowa, leafy spurge emergence was low (2% or less) from late April to late September, except in late August when emergence was 20% [27]. When freshly ripe seeds were sown in the summer in a North Dakota old field, 50% germinated the following spring. Of these, less than 10% were alive on 15 May [73].

Seedling morphology, physiology: Leafy spurge seedlings grow rapidly and are capable of vegetative regeneration soon after emergence. In the greenhouse, 2-day old leafy spurge seedlings were 0.7 inch (1.8 cm) tall with 2.5-inch (6.4 cm) long roots. At 24 days old, seedlings were 2.5 inches (6.4 cm) tall with 7-inch (18 cm) roots [200]. Hanson and Rudd [73] reported that roots of a "vigorous" leafy spurge seedling can reach 24 inches (61 cm) deep within 2 weeks of producing cotyledons.

Leafy spurge seedlings do not flower in their 1st year but are capable of vegetative regeneration within a week of emergence. Fifteen-day-old seedlings produced an average of 4.7 vegetative root buds. In the field, 5% of 7-day-old seedlings sprouted after being severed 1 inch (2.5 cm) below the soil surface [198,200]. The main leafy spurge seedling shoot usually does not survive beyond the 1st growing season and is replaced by an adventitious shoot from the root crown in the 2nd growing season [17].

Soil texture, moisture, fertility: Leafy spurge seedling emergence and survival can be higher on fine- than coarse-textured soils. In old fields in Saskatchewan, leafy spurge seedling densities of 2,800 seedlings/m^2 were common in the spring. As the growing season progressed, seedling densities typically decreased to 1,000 seedlings/m^2 on fine-textured soils and 500 seedlings/m^2 on coarse-textured soils. Dry conditions led to even greater seedling mortality [199].

Seedling shoot, lateral root, and root bud production can be greater on high- than low-nitrogen soils. Raju and others [176] reported poor seedling survival during extreme growing-season drought conditions. In the greenhouse, the height of leafy spurge seedlings at low nitrogen levels was about half that at high nitrogen levels, but length of the primary root increased slightly with nitrogen deficiency. Lateral root production was "greatly promoted" at high nitrogen levels, and the number of root buds averaged 59.9, 40.4, and 29.9 at high, medium, and low nitrogen levels. Following stem removal, regrowth averaged 7, 3.2, and 0.6 stems/pot at high, medium, and low nitrogen levels [141].

Soil disturbances and competing vegetation: Soil disturbances and low vegetation cover are associated with increased leafy spurge seedling establishment, growth, and survival. Vertical seedling root growth is more extensive, and production of root buds is earlier in areas with low vegetation cover or no associated vegetation than in areas with high cover [176]. In mixed-grass prairie in Manitoba, Canada, researchers located 83 distinct leafy spurge patches. Of these, 79 were associated with visible soil disturbance [14]. In the mixed-grass prairie on a military training site at Shilo, Manitoba, frequency of leafy spurge increased with increased frequency of bare ground [238].

In a field study near Regina, Saskatchewan, leafy spurge emergence and survival were greater in cultivated than undisturbed portions of a native grassland or western snowberry (*Symphoricarpos occidentalis*) patch. Emergence and survival of leafy spurge seedlings was lowest in undisturbed grassland. The only leafy spurge plants to flower in the 3rd growing season occurred in the cultivated plot [15]:

Emergence and survival of leafy spurge seeded* in disturbed and undisturbed habitats in Saskatchewan [15]

Habitat	Native grassland	Cultivated plot	Western snowberry patch
Total emergence after 2 years (no/m^2)	65	546	450
Total survival after 2 years (no/m^2)	36	406	122

*Seeding rate was 8,000 leafy spurge seeds/m^2 of habitat.

In a plowed and weeded area near Mandan, North Dakota, the early growth of leafy spurge plants from seeds was similar to early growth from root fragments. In dense crested wheatgrass and smooth brome, however, seedlings were significantly smaller than sprouts from root fragments. In the sod, no plants from seed or root produced flowers or more than 1 shoot by end of the 2nd growing season. In the plowed and weeded area, all plants from roots and 6 of 8 seedlings produced seed in the 1st growing season [149].

Height (cm) of leafy spurge plants in the 1st and 2nd growing seasons after planting seeds or root pieces in areas with and without interference from other plants [149]

	Sod	Plowed and kept weed free

Plant source		
	1st growing season (4 months after planting)	
Root	15b	44a
Seed	3c	34a
	2nd growing season (16 months after planting)	
Root	15a	67a
Seed	6b	62a
Values in the same column and growing season followed by different letters are significantly different ($P<0.05$).		

Vegetative regeneration: Leafy spurge can spread, regenerate, and reproduce prolifically from the root crown, root buds, and root pieces. Studies report very few limitations to successful vegetative regeneration. Very young and repeatedly damaged leafy spurge plants can regenerate. Small, deeply buried leafy spurge root pieces can develop into new plants. Spread by root growth and root sprouting is rapid and rampant. Leafy spurge persistence depends on vegetative regeneration.

Leafy spurge seedlings are capable of vegetative regeneration within a week of emergence. By 15 days old, leafy spurge seedlings had an average of 4.7 root buds. In the field, 5% of 7-day-old seedlings sprouted after being cut 1 inch (2.5 cm) below the soil surface. Plants emerging from root pieces can produce seed within 7 weeks of emergence [198,200].

In Saskatchewan, leafy spurge plants survived 8 years of shoot damage or removal by domestic sheep. After 8 years of grazing there were 5 to 10 leafy spurge shoots/m². Within 2 years of removing continuous grazing pressure, shoot densities were recovering to those levels present before intensive grazing [22].

Very small, partially dried, and deeply buried leafy spurge root fragments are capable of producing new plants. Three weeks after planting leafy spurge root pieces that ranged from 0.25 to 4 inches (0.6-10 cm) long in moist, clay soils outdoors in North Dakota, there was no emergence from the 0.25-inch pieces (0.6 cm), but 60% of the 0.5-inch (1.3 cm) pieces sprouted. Generally, the rate and height of shoot growth was positively correlated to root fragment size. Growth from the root pieces was rapid. Within about a month, 2-inch (5 cm) root pieces had developed stems that were 4 inches (10 cm) tall and roots that were 8 inches (20 cm) long. Within about 3 months, stems were 10 inches (25 cm) tall, vertical roots were 43 inches (109 cm) long, and horizontal roots were 12 inches (30.5 cm) long. No planted leafy spurge root fragments sprouted after being dried for 3 hours on a soil surface that was 106 to 118 °F (41-48 °C) and where the relative humidity was 45%. Only 1 of 20 root fragments dried to 13.4% moisture content produced sprouts [73].

Although the majority of shoots come from leafy spurge roots within the top 1 foot (0.3 m) of soil, excavation experiments revealed that regeneration is possible from deeply buried roots and from root fragments collected from great depths. On a leafy spurge plant excavated from a field in Iowa, a shoot was found growing from a root bud 10 feet (3 m) deep. The excavated plant was estimated at 10 years old [6]. A root piece obtained from a 48-inch (122 cm) depth sprouted, and during excavation, researchers found a shoot growing on a root 71 inches (180 cm) below the soil surface. When a leafy spurge plant was buried with 3 feet (1 m) of tamped, clean soil, shoots emerged within a year. Shoots also emerged within a year where plants and soil were excavated to a 3-foot (1 m) depth and the excavation area was filled with tamped, clean soil [40]. The survival of emerging shoots typically decreased with depth of burial, but shoots emerged for 5 successive years from 3-foot-deep (1 m) excavation areas [199].

Rates of vegetative spread: Through root growth and sprouting, leafy spurge can occupy a large area in a short time. Radial vegetative spread of a leafy spurge patch can be 0.5 to 11 feet (0.2-3 m) annually [198]. In a field in Saskatoon, Saskatchewan, where 100 leafy spurge seeds were planted, 7 seedlings emerged, and at the end of the growing season, seedlings occupied 2 ft² (0.2 m²). After 3 years, 223 ft² (21 m²) was occupied, and after 5 years, 470 ft² (44 m²) was occupied. Delayed germination as well as vegetative growth may have attributed to spread [199,200], and initial size of the seeded area was not reported. In Mandan, North Dakota, a single leafy spurge root fragment planted in an open area that was kept free of other vegetation occupied a 10-foot (3 m) diameter area in the first year [149]. Using a rudimentary patch expansion model together with patch density and spread information in the field, researchers estimated that a single leafy spurge plant could occupy 452 ft^2 (42 m^2) in 10 years, 3,300 ft^2 (300 m^2) in 20 years, and 4,000 m^2 in 63 years, assuming unrestricted growth [11]. In Saskatchewan, the average annual rate of spread was greatest (2.6 feet (0.8 m)) in an ungrazed native grassland and lowest (1.4 feet (0.4 m)) in a 3-year-old crested wheatgrass field. Individual patch size increases varied considerably; 1 especially vigorous patch occupied 7 ft^2 (0.6 m^2) in 1951 and 2,610 ft^2 (242 m^2) in 1956 [200]. Although some spread may have been due to seedling establishment, the contribution was likely low. Best and others [15] found that vegetative regeneration was more important than sexual reproduction to the persistence and spread of established leafy spurge stands. Findings are summarized below.

Emergence and survival of seedlings and vegetative sprouts on 3 plots of dense leafy spurge near Regina, Saskatchewan [15]			
Year	1975	1976	1977
Seedlings emerging/m^2	389	267	168
% of seedlings surviving to end of season	12	0	14
Shoots emerging from crown or root/m^2	355	0	365
% of vegetative shoots surviving to end of season	90	0	91

SITE CHARACTERISTICS:
Leafy spurge occurs on a variety of sites that include roadsides, old fields, pastures, meadows, riparian areas, and open woodlands [44,61,78,91,213]. In Saskatchewan leafy spurge occurs "in almost every conceivable habitat, with the exception of boreal forest" (reviews by [199,200]). Sand dunes, glacial moraines, eroded slopes, and saline depressions are all potential leafy spurge habitat [199].

Climate: Although leafy spurge is most common and problematic in semi-arid continental climates, it also occurs in xeric to subhumid and subtropical and subarctic climates [21,199]. In Saskatchewan, leafy spurge occurred in areas where high temperatures exceeded 100 °F (38 °C) and low temperatures dipped below -50 °F (-46 °C), annual precipitation ranged from 7 to 25 inches (180-630 mm), and the number of frost-free days averaged 106 [199]. During controlled experiments, survival of leafy spurge root crown buds was reduced by 50% at 10 °F (-12 °C) in one year and -4 °F (-20 °C) in another year [194].

Greenhouse experiments suggested that "competition" between leafy spurge, Kentucky bluegrass (*Poa pratensis*), and western wheatgrass (*Pascopyrum smithii*) could be less "intense" in years with frequent and substantial precipitation. Researchers indicated that the greenhouse findings may not be realized in the field, because only even-aged juvenile plants were tested and there were few height differences between leafy spurge and the grasses [186].

Elevation ranges reported for leafy spurge in parts of the western United States	
State	Elevation (feet)
California	<4,600 [78]
Colorado	5,000-6,500 [75]
Nevada	4,900-7000 [91]
Northern New Mexico	5,000-6,000 [131]
Utah	4,600-9,500 [234]

Soils: Leafy spurge occurs in a variety of soils ranging from rich, damp riparian soils to dry, nutrient-poor rangeland soils [17]. However, field surveys in Saskatchewan indicate that leafy spurge is most common on coarse-textured soils, and the size of leafy spurge infestations increases as soil textures change from clays to sands [199]. While plants may be more common, grow more rapidly, produce deeper roots, and be more difficult to control on coarse-textured soils [199], seedling emergence and survival are generally best in fine-textured soil (see Soil effects on seedling establishment section). Greenhouse studies showed that leafy spurge root biomass may be lower and may be concentrated in the upper soil profile when soil nitrogen levels are high [188]. Leafy spurge tolerates some flooding. Plants survived in 3 of 4 pots that were flooded for 4.5 months. At a field site in Saskatchewan, leafy spurge failed to survive 5 years of continuous flooding [200].

SUCCESSIONAL STATUS:
Although disturbed, open sites are best for leafy spurge seedling establishment, once established, vegetative regeneration allows for persistence in most habitats with or without subsequent disturbances. In Saskatchewan and Wisconsin, leafy spurge persists but may produce little or no seed in shaded habitats. Leafy spurge occurred in shaded woodland areas in Saskatchwan and Wisconsin. Shade was measured with a light meter, which read about 60 in open habitat. Leafy spurge occurred under a quaking aspen (*Populus tremuloides*) canopy where the light meter reading was 3; it flowered where the light reading was 6. It "flourishe(d)" in bur oak (*Quercus macrocarpa*) stands with 65% to 75% canopy cover and produced seed in areas with a light meter reading of 10. In Saskatchewan, leafy spurge spread "consistently" with competition from western snowberry. Vegetative spread of 2 leafy spurge seedlings in a western snowberry patch averaged about 1 foot (0.3 m)/year for 4 years [200]. Leafy spurge density increased "markedly" in 6 years of succession on a recently abandoned field in Saskatchewan. As succession progressed from annual to perennial species dominance, the percentage of leafy spurge shoots producing flowers decreased from 71% to 37% [199].

Disturbance relationships: Leafy spurge establishes well on disturbed sites but also in areas with little or no disturbance [178]. In southern Saskatchewan, 56% of leafy spurge populations occurred in areas under cultivation, 23% occurred in abandoned fields, and 21% occurred in areas that were never cultivated [199]. Once established, leafy spurge is highly tolerant of disturbance. In a field experiment, leafy spurge stem density increased with tilling. There were 134 leafy spurge stems/m² in the undisturbed plot and 316 stems/m² in the tilled plot [199]. Disturbed sites can serve as gateways into undisturbed stable vegetation. After leafy spurge established on a gopher mound in Saskatchewan, populations increased and persisted in "climax", ungrazed needlegrass-grama (*Stipa*-*Bouteloua* spp.) grasslands (reviews by [199,200]).

Cattle grazing can increase leafy spurge abundance. Heavy, continuous gazing by domestic sheep and goats can reduce leafy spurge abundance (see Importance to Livestock and Biological Control); once goats or sheep are removed, however, leafy spurge recovers. Cattle avoid leafy spurge and graze on associated vegetation, which can remove competition and provide open sites for subsequent leafy spurge establishment and spread [34,118]. In field experiments designed to simulate goat grazing in North Dakota's Sheyenne National Grasslands, leafy spurge cover increased significantly (P<0.05) when defoliated annually for 4 years at the vegetative and regrowth stages (mid-May and early September, respectively). Leafy spurge cover also increased significantly in unclipped plots. Stem densities were reduced by an average of 55% when defoliated twice a year for 4 years—once before flowering and again at the regrowth stage [94].

FIRE EFFECTS AND MANAGEMENT

SPECIES: Euphorbia esula

- FIRE EFFECTS
- FUELS AND FIRE REGIMES
- FIRE MANAGEMENT CONSIDERATIONS

Leafy spurge sprouts on a 2-year-old burn near Florence, Montana.
Photo © 2010 Katharine R. Stone.

FIRE EFFECTS:

Immediate fire effect on plant: Leafy spurge is typically only top-killed by fire [170,240]. Mortality of established plants by fire was not reported in the available literature (2010). Leafy spurge seeds and seedlings are sometimes killed by fire [83,224].

Postfire regeneration strategy [211]:
Geophyte, growing points deep in soil
Ground residual colonizer (on site, initial community)
Initial off-site colonizer (off site, initial community)

Fire adaptations and plant response to fire: Leafy spurge has a large, deep, and highly regenerative root system (see the earlier discussion on Vegetative regeneration), which makes postfire sprouting of established plants nearly certain.

Fire adaptations: Established leafy spurge plants survive fire. Because very deep leafy spurge roots are capable of sprouting, even severe fires are not likely to kill mature plants. A leafy spurge plant excavated from an Iowa old field produced shoot material from a root 10 feet (3 m) deep [6].

Leafy spurge seeds can be killed by fire. Fire timing, fire severity, and depth of seed burial may affect survival; however, the effects of fire season, fire severity, and depth of burial on seed and/or seedling survival were rarely evaluated or compared in the available literature (2010). In small-scale, controlled fire experiments, germination of leafy spurge seeds on the soil surface in burned trays was much lower than that of seeds in unburned trays. In unburned samples, nearly 50% of seeds on the soil surface germinated. When seeds were burned in trays with a crested wheatgrass litter fuel load of 100 g/m², germination was 7.6%. While emergence of a proportion of leafy spurge seeds was expected at any fuel load (up to 600 g/m²), the probability of emergence was often less than 0.01. The maximum soil surface temperature produced at any fuel load was less than 289 °F (143 °C) [224]. In North Dakota's Little Missouri National Grassland, germination of leafy spurge from soils collected on burned plots was significantly ($P<0.05$) less than that from unburned plots, and germination from spring-burned soils was less than that from fall-burned soils [240]. Findings are summarized below. More on this study is presented in Plant response to fire.

Germination of leafy spurge compared in soil samples collected from burned and unburned plots in North Dakota [240]		
Treatment	Germination (%) in soils from floodplain site	Germination (%) in soils from upland site
Spring fire	0.23a	0.73a
Fall fire	1.07b	2.47b
Unburned	4.93c	3.83c
Values within a column with different letters are significantly different (P<0.05).		

Plant response to fire: Postfire sprouting is common for mature leafy spurge, and leafy spurge abundance can be greater on burned than unburned sites. Fire's effect on leafy spurge seeds and seedlings is more variable. Reduced leafy spurge seed germination was reported after a spring fire in western North Dakota's Little Missouri National Grassland [83]. On 2 sites in east-central North Dakota, however, leafy spurge seedling density was high following spring prescribed fires. Survival beyond the seedling stage was not reported, but researchers suggested that fire could be useful in seed bank depletion [105].

Although the following studies indicate that leafy spurge is tolerant of fire, few studies compared the same sites before and after fire, sites burned at different severities, or short and long-term fire effects. After 6 years of surveying prairie remnants in Iowa's Loess Hills, Orwig [164] reported that leafy spurge "thrives and expands under a program of burn management". Barker (personal communication cited in [76]) reported that leafy spurge stem densities increased on sites burned in early May and on sites burned in early October in southeastern North Dakota's Sheyenne National Grasslands. Time since fire and other details were lacking. In the Little Missouri National Grassland, density of leafy spurge was similar on spring-burned, fall-burned, and unburned plots, measured the summer following treatments. Germination of leafy spurge seed collected from burned plots was significantly lower than that collected from unburned plots, and germination of seeds from spring-burned plots was significantly lower than that of seeds from fall-burned plots (P<0.05) [240].

Density of leafy spurge on burned and unburned plots across floodplain and upland sites in North Dakota [240]		
Treatment	Average leafy spurge density (number of stems/m²)	Approximate time since fire
Spring fire (4 May 1986)	364a	3 months
Fall fire (19 September 1985)	228a	15 months
Unburned	239a	N/A
Values within a column followed by the same letters are not significantly different (P<0.05).		

Several studies report little difference in leafy spurge abundance on burned and unburned sites. In Lancaster County, Nebraska, leafy spurge stem densities were significantly (P<0.04) greater in a tallgrass prairie after prescribed fires in mid May (84 stems/m²) than after prescribed fires in late May (27 stems/m²). However, stem densities in burned prairie were not different from unburned prairie regardless of fire timing [133]. Following a prescribed fire in mid-October on the Gilbert C Grafton South Military Reservation in North Dakota, leafy spurge postfire sprouting was "vigorous", but stem densities were not significantly different on burned and unburned plots 1 and 2 years after the fire [170].

Research for this review found that a study by Dix [47] was frequently cited as evidence that leafy spurge abundance may be reduced by fire. In this study, leafy spurge was absent from 3 burned plots but occurred with 17% frequency on 1 of 3 unburned plots in the badlands of western North Dakota. Plots were burned in late September 3 years before the evaluation of burned and unburned plots. The researcher drew no conclusions about leafy spurge and fire in this study, and the burned and unburned plots were separated by a draw and a distance of about 600 feet (183 m). Because burned and unburned plots were isolated spatially, and prefire data were lacking, study findings cannot be attributed to fire effects.

FUELS AND FIRE REGIMES:
Fuels: According to Bjugstad (personal communication 1987, cited in [17]), the high oil content of leafy spurge foliage allows for "good" fire spread, and an herbicide treatment prior to burning may improve flammability and/or fire spread. Senescing plants may support better fire spread than green plants.

Fire regimes: The effects of dense leafy spurge stands on fire frequency or fire severity were not described in any detail in the reviewed literature (as of 2010). Some have speculated that leafy spurge infestations can alter fire frequency [29], but the ways in which fire frequency was changed were not reported, and the studies or observations that support this assertion were not described. Some suggest that leafy spurge expanded its range rapidly with fire exclusion from grasslands in the northern Great Plains [24]. However, because leafy spurge introductions were occurring at about the same time as fire exclusion began (see discussion on North American introductions), the cause and effect relationships suggested by Brockway and others [24] may be purely coincidental. See the Fire Regime Table for additional information on the fire regimes in those habitat types or vegetation communities where leafy spurge may be abundant.

FIRE MANAGEMENT CONSIDERATIONS:
Potential for postfire establishment and spread: Although some leafy spurge seed mortality is likely on burned sites, there is high potential for postfire establishment from on- and off-site seed sources and vegetative spread into open sites. Leafy spurge produces abundant seed in most years, adds a small portion of seed to the soil seed bank, and disperses seed by ejection from the capsule, water transport, and animal movements. Open sites and soil disturbances are associated with increased leafy spurge seedling establishment, growth, and survival (see the discussion on Disturbances and seedling establishment).

Preventing postfire establishment and spread: Preventing invasive plants from establishing in weed-free burned areas is the most effective and least costly management method. This may be accomplished through early detection and eradication, careful monitoring and follow-up, and limiting dispersal of leafy spurge propagules into burned areas. General recommendations for preventing postfire establishment and spread of invasive plants include:

- Incorporate cost of weed prevention and management into fire rehabilitation plans
- Acquire restoration funding
- Include weed prevention education in fire training
- Minimize soil disturbance and vegetation removal during fire suppression and rehabilitation activities
- Minimize the use of retardants that may alter soil nutrient availability, such as those containing nitrogen and phosphorus
- Avoid areas dominated by high priority invasive plants when locating firelines, monitoring camps, staging areas, and helibases
- Clean equipment and vehicles prior to entering burned areas
- Regulate or prevent human and livestock entry into burned areas until desirable site vegetation has recovered sufficiently to resist invasion by undesirable vegetation
- Monitor burned areas and areas of significant disturbance or traffic from management activity
- Detect weeds early and eradicate before vegetative spread and/or seed dispersal
- Eradicate small patches and contain or control large infestations within or adjacent to the burned area
- Reestablish vegetation on bare ground as soon as possible
- Avoid use of fertilizers in postfire rehabilitation and restoration
- Use only certified weed-free seed mixes when revegetation is necessary

For more detailed information on these topics, see the following publications: [5,25,60,220].

Use of prescribed fire as a control agent: Prescribed fire alone is not used to control leafy spurge, but fire in conjunction with herbicides has provided some control, and fire may improve the effectiveness of flea beetle biocontrols.

Fire and herbicides: Eliminating woody or dead stems and ground litter with prescribed fire can be useful in increasing the visibility of small leafy spurge plants and seedlings and improving herbicide coverage [126]. In a tallgrass prairie restoration handbook, Solecki [205] suggests that leafy spurge can be controlled with repeated fall herbicide treatments followed by spring burning. Two to 3 herbicide and burning treatments were necessary for control, but the duration of control was not reported. Smith (personal communication 1987 cited in [17]) reported "excellent" control of leafy spurge after 5 to 6 years of biennial burning and herbicide treatments. Fire timing was not critical to control, but herbicide treatments needed to occur 3 to 4 weeks after burning.

Fire did not improve herbicide control of leafy spurge in 2 studies in North Dakota. In a mixed-grass prairie site at Gilbert C Grafton South Military Reservation, leafy spurge density was not significantly different on plots treated with herbicide only and plots treated with herbicide and burning ($P>0.05$) [170]. When unburned, burned, and combination (herbicide treated, then burned) treatments were compared in the Little Missouri National Grassland, leafy spurge density was lowest on combination plots, but combination treatments did not reduce stem density significantly more than herbicide treatments alone. However, leafy spurge germination was lower in soils collected from burned-only and combination plots than in soils collected from unburned or herbicide-only plots. Germination was lower on spring-burned than on fall-burned plots, regardless of herbicide treatments [240]. Leafy spurge abundance was still low and native grasses and forbs were reestablishing on plots 2 years after combination treatments (Bjugstad 1987 personal communication cited in [17]).

Fire and flea beetles (*Aphthona* spp.): Researchers found that fall or spring burning prior to the release of *A. nigriscutis* improved its colonization of leafy spurge-infested grasslands in south-central and southeastern North Dakota. Fires occurred in mid-October or early May, and beetles were released in late June of the following growing season. Within a year of the release, there were significantly more flea beetles on burned than unburned plots ($P<0.01$). Flea beetle colonization success was positively associated with percentage of bare ground and negatively associated with increasing litter depths. In this study, most beetle populations failed to persist past the first generation [54]. In another study, burning before releasing a large number of flea beetles showed immediate leafy spurge control benefits. Within a year of beetle release in plots burned in June, the average leafy spurge-free radius extended 37 inches (93 cm) from the release sites in burned plots and 14 inches (36 cm) in unburned plots. In burned plots, there was a zone of reduced stem density 10 to 13 feet (3-4 m) beyond the major defoliation area. Unburned plots lacked this additional reduction zone (Fellows unpublished data cited in [54]).

Some researchers report that fires from mid-May to mid-August could interfere with the life cycle of adult flea beetles in leafy spurge-infested areas [143]. However, the study conducted in North Dakota indicates that appropriately timed prescribed burning programs can occur without disrupting established flea beetle populations. When grassland sites with established *A. nigriscutis* populations were burned in the spring (mid-May) or fall (mid-October), there were no significant differences in flea beetle numbers within a year of burning. Researchers suggested that spring fires should occur early enough to allow for leafy spurge regrowth prior to beetle emergence. In southeastern North Dakota, emergence occurred around 25 May in most years but could be as early as 15 May in a dry year. Because the flea beetles have typically laid their eggs by early September, fall fires after this time should not harm flea beetle populations [54].

Altered fuel characteristics: The effects of dense leafy spurge stands on fire frequency or fire severity were not described in any detail in the reviewed literature (as of 2010). For a short discussion on this topic, see the Fuels and Fire regimes sections.

MANAGEMENT CONSIDERATIONS

SPECIES: Euphorbia esula

- FEDERAL LEGAL STATUS
- OTHER STATUS
- IMPORTANCE TO LIVESTOCK AND WILDLIFE
- OTHER USES
- IMPACTS AND CONTROL

FEDERAL LEGAL STATUS:
None

OTHER STATUS:
Information on state-level noxious weed status of plants in the United States is available at Plants database.

IMPORTANCE TO LIVESTOCK AND WILDLIFE:
Cattle and horses avoid leafy spurge, while domestic goats and sheep readily graze it. Leafy spurge seeds are consumed by mourning doves [6], and nesting success of western meadowlarks was positively associated with leafy spurge cover in North Dakota [193]. More information about leafy spurge Palatability and/or nutritional value is provided below.

Cattle avoid grazing leafy spurge and will focus on other vegetation in infested areas; this selective grazing can promote leafy spurge spread and seedling establishment [34,118]. In Grassrange, Montana, cattle avoided grazing in areas with moderate to high leafy spurge abundance [77]. In southeastern North Dakota, cattle grazed only in areas without leafy spurge early in the growing season. In mid-summer, cattle avoided areas with moderate to high leafy spurge densities and utilized just 2% of the vegetation in areas with low leafy spurge density, even though stocking rates exceeded the recommended rates by 21%. In the fall, utilization of leafy spurge-infested areas increased to 60%, 50%, and 41% in areas with low, moderate, and high densities of leafy spurge [119].

The milky sap produced by leafy spurge can cause severe diarrhea in cattle and horses. However, leafy spurge is avoided by these animals unless no other forage is available. Leafy spurge sap can also cause blistering and hair loss around horses' hooves. This type of injury is common if horses are put in a recently mowed, leafy spurge-infested pasture [15].

Domestic sheep and goats are not typically harmed by grazing leafy spurge and have been successfully used to control it (see the Biological control section). In central Montana, domestic sheep grazed all phenological stages of leafy spurge in infested areas and suffered no ill effects or substantial weight loss [103]. However, in a leafy spurge-infested area near Pearce, Alberta, sheep grazed small plants but were "reluctant" to graze mature plants. Researchers reported that some sheep died of leafy spurge poisoning in the first year of grazing relatively large plants [86]. In North Dakota's Sheyenne National Grasslands, angora goats grazed areas where leafy spurge and Kentucky bluegrass together made up 44% to 69% of the total available forage. Leafy spurge made up more than 40% of goat diets and more than 50% of all fecal collections over a 2-year period [95].

Domestic sheep and goats as well as native ungulates are potential dispersers of leafy spurge seed. For details, see Seed dispersal.

Birds: Leafy spurge seed is consumed by mourning doves [6] and provides suitable nesting habitat for western meadowlarks. In North Dakota's Sheyenne National Grassland, western meadowlark nesting success was positively related to leafy spurge cover [193]. Other bird populations and their nesting success were negatively related to leafy spurge abundance. For more information, see Impacts on wildlife.

Bees: Beekeepers use leafy spurge as an early-season honeybee food. Honey produced by bees feeding on leafy spurge is bitter. Leafy spurge honey is fed back to bees in the winter because it freezes at a lower temperature than honey from other sources [118].

Palatability and/or nutritional value: Lym [118] reports that leafy spurge is an "acceptable and nutritious" food for domestic sheep and goats. Leafy spurge elaiosomes removed by western thatching ants in Park County, Montana, were 25.4 % fat and 18.2% protein [165].

Researchers compared the nutritional value of leafy spurge and alfalfa (*Medicago sativa*) throughout the growing season in various North Dakota locations and found that nutrient levels were adequate for young, mature, and nursing domestic sheep and goats. The study did not evaluate whether nutritional value impacted palatability [92]. In Montana's Gallatin County, growing-season crude protein and digestibility of leafy spurge were almost always higher than those of Idaho fescue (*Festuca idahoensis*) [158].

McDonnell [139], director of market information and public lands for the American Sheep Industry Association, reported that leafy spurge protein levels are higher than those of many grasses in the spring and summer. According to McDonnell [139], weight gains for ewes grazing leafy spurge were not different than those grazing grasses. Lambing difficulties, including reduced lamb weights or reduced lamb percentages, were not reported when sheep were grazing leafy spurge. Young lambs grazing leafy spurge had significantly higher average daily weight gains than lambs grazing grass. In studies from Idaho to North Dakota, researchers found that soil fertility may affect leafy spurge palatability. Domestic sheep preferred leafy spurge on highly fertile sites [97].

OTHER USES:
Leafy spurge may be potentially useful as a biofuel [137], medicine [150], or pest control agent [241]. Researchers isolated dipterpenes from leafy spurge that showed antiviral properties against herpes simplex [150]. In China, a dilution from boiled leafy spurge plant material has been used to control maggots, mosquito larvae, rats, and some plant diseases.

IMPACTS AND CONTROL:
Impacts: Leafy spurge is considered a "serious", "very aggressive", "most troublesome", and "highly invasive" nonnative species in the northern half of the United States [61,91,99,218], which has established and spread in stable, undisturbed native plant communities [44,132]. In Minnesota's Pipestone National Monument, leafy spurge is the highest control priority because delayed control results in the great costs [180]. In Massachusetts, leafy spurge has spread into native or minimally managed plant communities [132]. At the coastal and southern fringes of its US distribution (see General Distribution), leafy spurge is less aggressive and less problematic for land managers. In Virginia, leafy spurge is "occasionally invasive", typically establishes only in "severely" disturbed areas, and spreads slowly or not at all from disturbed sites [225].

Leafy spurge's high reproductive rates, potential for rapid dispersal, and already large, established populations in natural areas make it a severe threat to native plant communities (Hiebert and Stubbendieck 1993 cited in [180]). As of 2000, leafy spurge was among the 10 most frequently listed noxious weeds in the contiguous United States and Canada's southern provinces [204]. As of 2005, leafy spurge ranked 6th in a list of 81 nonnative, invasive species seriously impacting natural habitats of Canada [35]. In a survey of Wisconsin's authorities on local flora, leafy spurge ranked 12th out of 66 nonnative invasive plants evaluated for their impacts on native plant communities [183].

Observations, surveys, and studies indicate that leafy spurge establishment, spread, and persistence can negatively impact human health, native and rare plant species abundance, ranching and farming economies, wildlife abundance and land use patterns, and competition for pollinators. One study suggests that leafy spurge's US distribution may contract with future climate changes, but another study suggests that leafy spurge may become more invasive as CO_2 levels reach future predicted levels.

Impacts to human health: A review reports that leafy spurge contains toxins, likely within its milky sap, that can cause internal and external irritations. Swelling and burning of the mouth and throat and abdominal pain have been reported after ingestion of leafy spurge. Blisters and skin inflammation can occur after handling leafy spurge [118]. Severe dermatitis has been reported for some people [15]. After researchers identified tumor-promoting properties in leafy spurge, some have suggested a dietary cancer risk in eating livestock that graze leafy spurge (review by [118]). In the reviewed literature, no other studies evaluated this risk.

Impacts on associated vegetation: Rapid vegetative spread (see Rates of vegetative spread), dense stand production, and thick litter accumulations allow leafy spurge to replace rare and/or native plant species. In leafy spurge stands, densities of 1,000 stems/yd² are common. Researchers suggest that stands of that density could easily crowd out associated native vegetation [21]. The thick litter layer produced in dense leafy spurge stands can inhibit establishment of light-demanding species [231]. Other studies suggest that leafy spurge allelopathy or effects on soils and soil biota may also limit associated vegetation.

Studies indicate that leafy spurge threatens sensitive species, replaces native species, and negatively impacts species richness. In tallgrass prairie swales in North Dakota's Sheyenne National Grassland, leafy spurge often dominates and is "continuing to expand" in habitats that support the federally threatened Great Plains white fringed orchid (*Platanthera praeclara*). Future spread and efforts to control leafy spurge are considered serious threats to the orchid [202,203]. When the composition of remnant mixed-grass prairie and leafy spurge-dominated sites were compared in Manitoba, Canada, cover of common native species and total species richness were significantly greater ($P<0.05$) in prairie than leafy spurge-dominated vegetation. Areas beyond leafy spurge patches supported 7 to 11 native species, whereas areas where leafy spurge was abundant supported only 4 native species [14]. In 7 of 11 leafy spurge-infested plant associations in North Dakota's Theodore Roosevelt National Park, species richness was 51% lower in infested than uninfested areas. Species richness losses were greatest in silver sagebrush, creeping juniper, and prairie sandreed associations ($P<0.05$). While 77% to 93% of the species occurring in infested stands also occurred in uninfested stands, just 50% to 79% of the species in uninfested stands also occurred in infested stands. Across all communities, 93 species were restricted to uninfested stands. Of these, 53% were forbs, 25% were graminoids, and 21% were shrubs or subshrubs [29].

Allelopathy: Allelopathic effects could play a part in leafy spurge's impact on neighboring vegetation, but field studies documenting allelopathic influence are lacking. In Fort Collins, Colorado, high densities and frequencies of quackgrass (*Elymus repens*) and annual ragweed (*Ambrosia artemisiifolia*) occurred near the perimeter but were absent near the center of a leafy spurge patch. A follow-up greenhouse study found that growth of tomato (*Lycopersicon esculentum*) and hairy crabgrass (*Digitaria sanguinalis*) were greater in soils without leafy spurge litter than in soils with leafy spurge litter. Researchers suggested that dead or decaying leafy spurge plant material may have allelopathic properties [208]. In other laboratory studies, germination of common wheat (*Triticum vulgare*), crested wheatgrass, smooth brome, and wild mustard (*Sinapis arvensis subsp. arvensis*) watered with extracts of leafy spurge leaves or stems was significantly lower than that of controls ($P<0.05$) [200]. Growth of mouseear cress (*Arabidopsis thaliana*) seedlings treated with leafy spurge root exudate was lower than control seedlings. Researchers identified leafy spurge root compounds capable of causing necrosis or limiting root growth [173]. However, not all studies found evidence of allelopathy. A controlled study by Olson and Wallander [162] found little to no effect of leafy spurge litter leachate or leafy spurge-infested soils on germination, seedling growth, or seedling survival of bluebunch wheatgrass or western wheatgrass.

Soils and soil biota: Impacts of leafy spurge on associated vegetation may be related to changes in soils or soil biota from leafy spurge dominance or leafy spurge control and management. In Rocky Mountain National Park, Colorado, researchers conducted pairwise comparisons between mountain meadows dominated by leafy spurge and meadows with low leafy spurge abundance. Leafy spurge-dominated areas had been mechanically and chemically treated. There were significantly more native plants on uninfested than infested plots ($P=0.043$). There were more nonnative species on infested than uninfested plots, although differences were not significant. The number of soil microarthropods was significantly greater on uninfested than infested plots ($P<0.05$) [168].

In a greenhouse study, plant growth was compared in soils taken from containers where either leafy spurge, smooth brome, or native species were grown. Growth of white heath aster (*Symphyotrichum ericoides* var. *ericoides*), Lewis flax (*Linum lewisii*), upright prairie coneflower (*Ratibida columnifera*), and prairie Junegrass (*Koeleria pyramidata*) seedlings was lower in soils from pots with leafy spurge than in soils from pots with native species. Blue grama (*Bouteloua gracilis*) and green needlegrass (*Nassella viridula*) seedling growth was similar in soils from pots with leafy spurge and soils from pots with native species. Leafy spurge seedling growth was lower in soils from pots with native species than in soils from pots with smooth brome [87].

Many studies have attempted to estimate the economic impacts of leafy spurge invasion. While

Economic impacts:
most studies evaluated land value changes associated with reductions in cattle carrying capacities, others included reductions related to wildlife-associated recreation, soil and water conservation, as well as other social and environmental impacts. In North Dakota, researchers assessed the economic impacts of leafy spurge on wildlands. At the leafy spurge infestation levels present in the early 1990s, the direct economic impacts on wildlife-associated recreation, soil and water conservation, and other intangible benefits amounted to 3.6 million dollars. When evaluated with other direct and secondary economic impacts on wildlands and rangelands, costs were estimated at over 87 million dollars [230].

Value of ranch land in North Dakota that was heavily infested with leafy spurge was reduced by 60 to 85 dollars/acre based on reductions in livestock carrying capacity (Weiser 1995 cited in [159]). In the mid 1980s, the sale price of a large ranch in Klamath County, Oregon, was reduced by 83% because of leafy spurge infestations (Begley 1998 cited in [46], Weiser 1995 cited in [159]). Although the sale stipulated that the new owner must control the leafy spurge, 6 years and 60,000 dollars later there was little control (Weiser 1995 cited in [159]). Rinella and Luschei [184] developed models to estimate the economic impacts of leafy spurge at local and regional scales. For a 17-state area west of Minnesota and Texas, the model estimated that leafy spurge reduced the cattle carrying capacity by 50,000 to 217,000 cows/year and decreased the value of grazing lands by 8 to 34 million dollars/year [184].

Additional information is available on the economic impacts of leafy spurge in North Dakota [109,110] and the upper Great Plains [111]; on the economic impacts of leafy spurge on wildlands in Montana, South Dakota, and Wyoming [8]; on the social and economic impacts of leafy spurge in Montana [182]; on the social and economic impacts of leafy spurge on public lands in North Dakota and Montana [127]; and on the regional environmental, economic, and societal impacts of invasive species, including leafy spurge [48].

Impacts on wildlife: Leafy spurge was associated with reduced habitat utilization by ungulates in North Dakota, as well as low abundance and/or nesting success for several bird species in North Dakota and Manitoba. For 2 years in North Dakota's Theodore Roosevelt National Park, researchers compared ungulate use of leafy spurge-infested and uninfested habitats. Bison and deer (white-tailed deer and mule deer) pellet group densities were significantly (P<0.001) lower on infested than uninfested sites. Elk pellet group densities averaged 81% lower on infested than uninfested sites (P<0.1) [214]. In North Dakota's Sheyenne National Grassland, researchers surveyed grassland breeding bird densities and nesting success on plots with low (<20%), medium (20-60%), and high (>60%) cover of leafy spurge. Grasshopper sparrow and savannah sparrow densities were significantly lower on plots with high cover than those with medium or low cover (P<0.05). Densities of bobolinks and western meadowlarks were not significantly different on plots with low, medium, or high cover. Low-cover plots averaged 63 nests and 24 species; medium-cover plots averaged 57 nests and 26 species; and high-cover plots averaged 37 nests and 15 species [193]. In Manitoba, upland sandpipers and Sprague's pipits were significantly more abundant in native- than nonnative-dominated vegetation (P<0.05), but the opposite was true for grasshopper sparrows (P=0.059). Native prairie was dominated by blue grama, obtuse sedge (*Carex obtusata*), and porcupine grass (*Hesperostipa spartea*). Nonnative vegetation was dominated by smooth brome, Kentucky bluegrass, and leafy spurge. Cover of leafy spurge ranged from 17% to 81% [239].

Pollinators: Study findings are mixed regarding leafy spurge's effects on competition for pollinators. When insect visitation and pollen deposition were evaluated in leafy spurge-infested and uninfested prairies in Theodore Roosevelt National Park, competition for pollinators was not widespread and varied annually. In some years, native halictid bees visited infested prairies less frequently than uninfested prairies. Researchers suggested that pollination of rare species could be limited by the combined reductions in native flower density and conspecific pollen transfer [108]. Observations together with greenhouse and field experiments indicate that although leafy spurge and prairie violet (*Viola pedatifida*) share pollinators, evidence of pollination competition between the species was lacking. Prairie violet seed set was reduced when leafy spurge pollen was applied to flowers before successful pollination by conspecific pollen. Prairie violet received significantly more leafy spurge pollen on sites with than without leafy spurge (P<0.05). However, prairie violet fruit set was significantly higher on sites with than without leafy spurge (P=0.004) [145].

Climate change: Predicted future changes in climate may differentially affect leafy spurge's future distribution and invasiveness. Increases in CO levels may increase the invasibility of sites or the competitiveness of leafy spurge. A greenhouse experiment demonstrated that leafy spurge leaf and stem weights increased significantly at past, present, and predicted future CO_2 levels [243]. However, responses of associated native species were not investigated. Using bioclimatic modeling, researchers predict that the risk of invasion by leafy spurge could decrease in Colorado, Nebraska, Minnesota, and parts of Idaho and Oregon, but could increase in Canada [23].

Control: In their review, Hansen and others [71] report that leafy spurge is "extremely difficult to control with herbicides" and "almost impossible to control by cultural or physical methods". Many sources indicate that prioritizing control is important to successful management. Weed control handbooks and management guides report that early detection of new and small leafy spurge populations should be a top control priority, because well established populations are rarely controlled by any contemporary methods [21,46].

Land managers and researchers suggest that small leafy spurge patches should be treated before focusing on large populations, and that broadcast treatments for large infestations are largely unsuccessful. Lym and Zollinger [126] suggest mapping leafy spurge populations, protecting uninfested areas, treating small infestations first, and treating large populations from the outside edges inward. Researchers found that small leafy spurge patches in Saskatchewan increased in size at a much greater rate than large patches. In 5 years, a 7-ft² (0.6 m²) patch increased in area by 387 times, while a 701-ft² (65 m²) patch increased by 30 times. Assuming a lateral spread rate of 2 feet (0.6 m)/year for 5 years, a 0.5-foot (0.2 m) diameter patch would increase almost 500 times as fast as a 25-foot (7.6 m) diameter patch [199]. Using spatial growth models, researchers found that control could be improved by focusing on the elimination of satellite populations before treating large infestations. Control was "greatly improved" by eliminating just 30% of satellite populations [146].

Persistence, monitoring, and evaluating and adjusting methods are essential to long-term management of leafy spurge [100]. Leafy spurge sprouts emerge from surviving root portions even after elimination of all aboveground tissue. Monitoring and follow-up treatments may be necessary for up to 10 years after aboveground removal [17]. Control of biotic invasions is most effective when it employs a long-term, ecosystem-wide strategy rather than a tactical approach focused on battling individual invaders [128]. Various control methods and procedures are discussed by Lajenuesse and others [100], and Maxwell and others [138] developed a leafy spurge population model that assesses management strategies and allows managers to target leafy spurge's most vulnerable life stages.

In all cases where invasive species are targeted for control, no matter what method is employed, the potential for other invasive species to fill their void must be considered [26]. In biocontrol release areas in east-central and southeastern North Dakota, leafy spurge densities were reduced by 51% to 98%, but there was "little evidence" that leafy spurge was being replaced by desirable native species [107]. In Montana's Carter County, researchers found that nonnative species, primarily bluegrass (*Poa* spp.), replaced leafy spurge after its control by flea beetles. Although the flea beetles reduced leafy spurge cover and increased total vegetation abundance, there was little change in plant species composition or relative cover. Increases in total vegetation cover were primarily attributed to increases in nonnative species [31]. On the Altamont Prairie Preserve in eastern South Dakota, leafy spurge plots were grazed at high intensity for 4 years by goats or sheep. Flea beetles were released in the grazed area and within 5 years of their introduction, leafy spurge cover was reduced significantly ($P<0.001$). However, there were no dramatic increases in species richness associated with reductions in leafy spurge [39].

Prevention: It is commonly argued that the most cost-efficient and effective method of managing invasive species is to prevent their establishment and spread by maintaining "healthy" natural communities [128,201] (e.g., avoid road building in wildlands [216]) and by monitoring several times each year [85]. Managing to maintain the integrity of the native plant community and mitigating the factors enhancing ecosystem invasibility are likely to be more effective than managing solely to control the invader [82].

Weed prevention and control can be incorporated into many types of management plans, including those for logging and site preparation, grazing allotments, recreation management, research projects, road building and maintenance, and fire management [220]. Cleaning the seeds and root pieces from equipment before moving it into an uninfested area is important to preventing the establishment of new leafy spurge populations [46]. See the Guide to noxious weed prevention practices [220] for specific guidelines in preventing the spread of weed seeds and propagules under different management conditions.

Fire: For information on the use of prescribed fire to control this species, see Fire Management Considerations.

Cultural control: In a review, Hansen and others [71] reported that leafy spurge is "almost impossible to control by cultural or physical methods". While cultural control methods alone are unlikely to control leafy spurge, some management success has been reported with the combined use of cultural and chemical methods (see Integrated management).

Physical or mechanical control: Repeated cutting or mowing can limit leafy spurge seed production but may not reduce leafy spurge or restrict vegetative spread [17,46]. The milky sap in leafy spurge stems can build up in equipment, making it less effective and more difficult to operate [13].

Biological control: Domestic sheep and goats as well as a variety of insects have been used to control leafy spurge. While continued grazing by domestic sheep and goats is often successful in reducing leafy spurge stem abundance, roots survive and plants may still spread vegetatively [46,139,231]. Leafy spurge typically recovers when grazing pressure is removed [139,231]. Of the many Eurasian insects introduced to the United States and Canada to control leafy spurge, flea beetles have been most successful in providing long-term control thus far (2010). The use of pathogens or fungi in the biological control of leafy spurge has been studied, but as of 2010, none has been released [74,126,242].

Domestic sheep and goats: Control of aboveground growth and seed production are commonly reported in leafy spurge grazing management studies. After 4 years of continuous grazing by domestic sheep in Saskatchewan, leafy spurge shoot density was lower on grazed than ungrazed plots. After 8 years of grazing, the density of leafy spurge shoots was 5 to 10 shoots/m², and the seed bank density was 15 seeds/m². Within 2 years of removing grazing pressure, leafy spurge density was recovering [22]. After 4 or 5 years of domestic sheep grazing near Pearce, Alberta, basal area of leafy spurge decreased significantly, and basal area of crested wheatgrass increased significantly ($P<0.05$). Sheep avoided mature leafy spurge plants, and some poisoning occurred (for details, see the Livestock section above) [86]. After 2 years of domestic sheep grazing in Gallatin County, Montana, leafy spurge seedling density was reduced significantly ($P<0.0001$), and the number of viable leafy spurge seeds was reduced by 65%, which was a significantly larger decrease than that on ungrazed sites ($P<0.009$). Density of mature leafy spurge was not affected in 2 years of grazing, but density of Idaho fescue increased significantly ($P<0.0002$). However, grazing decreased the density of bluebunch wheatgrass ($P<0.08$) and increased the frequency of annual brome grasses ($P<0.02$) [160]. It is important to note that domestic sheep and goats can pass and disperse viable leafy spurge seed. These grazing animals should be kept from uninfested areas until leafy spurge seeds have passed, which was determined to be 5 days for goats and 9 days for sheep in a controlled feeding study [98]. Studies indicate that sometimes utilization differences exist between sheep with and without prior experience grazing leafy spurge [158,228].

Studies reported conflicting findings about prior exposure and learned behavior as it relates to leafy spurge control by domestic sheep. In Montana's Gallatin County, differences in leafy spurge grazing by naive and experienced yearlings was short-lived. In early summer, experienced yearlings grazed leafy spurge 4 times as much as naive yearlings, but by the 25th day of grazing, the 2 yearling groups grazed leafy spurge similarly [158]. In another study, experience increased leafy spurge utilization by sheep. Leafy spurge at a late phenological stage was grazed better by experienced than inexperienced sheep [228].

During confined feeding and field grazing studies on the upper Snake River Plains in southeast Idaho, domestic goats preferred leafy spurge more than sheep did. Goats concentrated on leafy spurge and avoided grasses ($P<0.03$), while the opposite was true for sheep. Within 8 weeks of grazing trials, leafy spurge was taller ($P=0.07$) and produced more flowers ($P=0.04$) in sheep-grazed than goat-grazed pastures [229]. In mesic to wet tallgrass prairie on South Dakota's Altamont Prairie Preserve, goat grazing resulted in greater leafy spurge control than sheep grazing. In 4 years of high-intensity grazing, leafy spurge cover increased by almost 30% in sheep-grazed pasture, was nearly unchanged in goat-grazed pasture, and nearly doubled in ungrazed pasture ($P<0.001$) [39].

Because domestic goats prefer forbs over grasses, leafy spurge often decreased and graminoids often increased with goat grazing. However, desirable forbs and shrubs can be reduced by domestic goats. After 3 or 4 years of grazing by angora goats in prairie and open woodland sites in Eddy County, North Dakota, leafy spurge frequency decreased and graminoid frequency increased significantly ($P<0.05$). Goat stocking was increased each year, and leafy spurge density was reduced by 12.5% and 84.2% after 1 and 4 years of grazing, respectively [195]. In Montana, researchers tested shock collars and invisible fencing to contain goats in leafy spurge-infested areas. While the containment method was successful and leafy spurge comprised the majority of goat diets, "brush and forb species were significantly impacted" [140]. After 3 years of grazing in mixed-grass prairie at a North Dakota National Guard training area, leafy spurge stem densities were unchanged in the cattle-grazed plot, reduced by 70% in the goat-grazed plot ($P<0.05$), and reduced by 60% in the cattle- and goat-grazed plot ($P<0.05$). Graminoid herbage production was unchanged by cattle grazing, increased significantly with goat grazing, and decreased significantly with goat and cattle grazing ($P<0.05$). Shrub utilization was not different among the grazed plots [171].

Several studies evaluated the economics associated with control of leafy spurge by domestic sheep. An economic feasibility study found that the addition of sheep to cattle ranches in Montana yielded positive returns when leafy spurge infested just 10% of a pasture. Positive returns increased with increased leafy spurge abundance and when infestations were concentrated on a few pastures [236]. In another study, Sell and others [197] estimated the economics related to cooperative fall, winter, or spring sheep grazing operations. Only spring grazing showed the potential to generate income, and this potential decreased as acreage infested by leafy spurge increased. Bangsund and others [10] found the economics of different grazing scenarios varied with carrying capacities, leafy spurge spread rates, rangeland productivities, fencing costs, and grazing patterns.

Insects: Many Eurasian insects have been approved and released for biological control of leafy spurge. Insects established in the United States include the leafy spurge hawk moth (*Hyles euphorbiae*), the red-headed leafy spurge stem borer (*Oberea erythrocephala*), the leafy spurge tip gall midge (*Spurgia esulae*), and 5 flea beetle species: *Aphthona cyparissiae*, *A. czwalinae*, *A. flava*, *A. lacertosa*, and *A. nigriscutis* [63,64,65,66,67,68,69,70,72]. By 1996, at least 1 of these insects was established in each of 18 states and 148 counties and produced collectable populations in 16 states and 62 counties [72].

Leafy spurge hawk moth larvae feed on leaves and bracts and are established from Idaho to Nebraska and Minnesota. Alone, leafy spurge hawk moths are ineffective controls [68]. Red-headed leafy spurge stem borer larvae feed in leafy spurge stems and crowns, and adults feed on leaves and stems. As of 2004, stem borers had not "noticeabl(y)" impacted leafy spurge, although established from Oregon to Colorado and Minnesota [69]. Leafy spurge tip gall midge larvae attack leafy spurge growing points and reduce flower and seed production. Gall midges disperse long distances, and as of 2004, occurred from Idaho to Colorado and east to Rhode Island [70]. Flea beetle larvae feed on leafy spurge root hairs and young roots, and adults feed on leaves and flowers. Information about the distribution, biology, ecology, establishment, spread, preferred habitats, and control success for leafy spurge biocontrols in North America is summarized in the following sources: [38,72,157,181].

Flea beetles: So far (2010), flea beetles are the most successful biocontrol agents for leafy spurge in North America [72,157]. As of 2004, flea beetle populations were established nearly throughout the western United States, the northern Great Plains, the Great Lakes states, and in the northeastern states of New York, Rhode Island, and New Hampshire [63,64,65,66,67]. Because flea beetles have provided the most effective control of leafy spurge, they are the most widely dispersed and most studied of the biocontrol insects. Although flea beetles do not eradicate leafy spurge, they can reduce its abundance and negative impacts [143]. An abundance of information is available about flea beetle habitat requirements, population dynamics, maintenance, persistence, and effects on leafy spurge populations. While some information regarding these topics is summarized in the discussions below, the bulk is summarized and described in bibliographical form in Table 1.

Successful flea beetle establishment requires knowledge of their habitat requirements, which are often related to leafy spurge stem densities, soils, and climate. Some studies report good control of leafy spurge by flea beetles in areas with soil-borne pathogens, such as *Rhizoctonia solani* and *Fusarium* spp. In the greenhouse, leafy spurge damage was more rapid when pathogens and insects occurred together than when either agent occurred alone. The researcher suggested that screening for or adding soil pathogens to flea beetle release sites could improve biocontrol [32,33]. In general, optimal flea beetle release sites occur on south-facing, sunny slopes with dry, loamy soils; however, there are species-specific differences. For instance, *A. lacertosa* establishes on cool, moist sites and may establish well in draws. Recommended release dates are from mid-June to mid-July, and establishment improves with increased abundance of flea beetles released. At least 1,000 beetles/drop point is recommended. Releasing flea beetles at the edge of dense leafy spurge patches or in sparse points within patches is typically better than releasing them within dense stands. For more information on monitoring, harvesting, storing, transporting, and rereleasing flea beetles, as well as guidelines for integrated control that ensures maintenance of established flea beetle populations, see the review by Merritt and others [143]. Additional information on species-specific habitat preferences is available in Table 2.

Flea beetles can be persistent and provide long-term leafy spurge control; however, control success can vary by site and flea beetle species. On 2 of 3 sites in east-central North Dakota, flea beetle populations were still present and leafy spurge was reduced substantially, even though releases were made 11 to 16 years earlier. Populations of *A. lacertosa* and *A. czwalinae* were much larger than those of *A. nigriscutis*, which had not substantially impacted leafy spurge [105]. Findings were similar along railroad rights of way in North Dakota. Within 4 years of release, *A. czwalinae* and *A. lacertosa* populations averaged 79 beetles/m², resulted in leafy spurge stem density reductions of 95% or more, and were impacting leafy spurge more than 330 feet (100 m) from the release site. Within 5 years of release, *A. nigristicus* populations resulted in leafy spurge stem density reductions of about 60%, although populations never exceeded 10 beetles/m², and impacted leafy spurge only 52 feet (16 m) from the release site [122].

Although flea beetles often decreased abundance of leafy spurge, this decreased abundance can negatively affect flea beetle populations and may not be associated with the recovery of desirable and diverse native plant communities. For 6 years, researchers monitored the establishment and effects of flea beetles on many sites in northwestern South Dakota and southeastern Montana. *Aphthona lacertosa* and *A. czwalinae* established on a variety of grassland and shrubland vegetation types; *A. nigriscutis* was less common and restricted to dry, sandy sites. Leafy spurge cover on and near release sites was significantly lower than prerelease levels ($P<0.05$). However, as cover of established leafy spurge plants decreased, seedling abundance increased and flea beetle abundance decreased. Grass species cover increased, but the same was not true for forb species [30]. Within 5 years of releasing flea beetles in North Dakota's Little Missouri National Grasslands, leafy spurge stem density was reduced by 90%, and its emergence from soil collected at release sites decreased from 68% to 14%. Abundance of other forbs in the soil at release sites increased, but increases were largest for less desirable and nonnative forbs. The percentage and number of desirable grasses in the soil at release sites decreased. In the greenhouse, the combined average production of green needlegrass, little bluestem (*Schizachyrium scoparium*), switchgrass (*Panicum virgatum*), and western wheatgrass was significantly ($P<0.05$) less in soils from release sites than from non-release sites after 8 weeks of growth. At both the release and nonrelease sites, leafy spurge densities were low [36]. Leafy spurge biomass and crown and stem densities were reduced by 60% to 80% with 2 years of inundative flea beetle releases (50 beetles/flowering stem) in riparian areas in Idaho. Cover of other forbs and grasses, however, did not increase [169].

Additional studies and their evaluations on leafy spurge and flea beetle populations are available. Consult Table 1 for a list of these studies and a brief summary of the information they provide.

Biological control of invasive species has a long history that indicates many factors must be considered before using biological controls. Refer to these sources: [223,237] and the Weed control methods handbook [215] for background information and important considerations for developing and implementing biological control programs. Lym [117] provides a review of the biological control of leafy spurge using insects, sheep, and/or goats.

Chemical control: Many sources provide information about the types of chemicals, timing of herbicide applications, and application techniques that are potentially useful in controlling leafy spurge: [2,17,114,116,117]. These studies and reviews are not summarized in detail in this review. See the Weed control methods handbook [215] for considerations on the use of herbicides in natural areas and detailed information on specific chemicals.

Long-term control of leafy spurge, especially large, well-established populations, is unlikely with herbicides alone. In a review, Hansen and others [71] reported that leafy spurge is "extremely difficult to control with herbicides", because of its ability to "purge" chemicals from its root system. In controlled studies, less than 7% of the picloram that was applied to the aboveground portions of leafy spurge occurred in the roots. More than 60% of the chemical had been released and was found in the area surrounding leafy spurge roots [79]. A waxy protective layer on leafy spurge leaves and stems also makes chemical control difficult without addition of a surfactant or wetting agent [58]. Although some indicate that proper timing of herbicide applications can improve control and prevent seed production (Messersmith personal communication cited in [1,76,206]), long-term control of leafy spurge with herbicides alone is unlikely and often economically infeasible. For more information on potentially improving the timing of chemical treatments, see Root carbohydrate storage.

Studies have uncovered several issues related to the control of leafy spurge with herbicides. These issues include the need for continual treatments, lack of long-term control, detrimental effects on associated vegetation, and high treatment costs. In tallgrass prairie in North Dakota, leafy spurge still dominated the seed bank the year after 2 applications of various herbicides, suggesting that it was likely to dominate the recovering vegetation [96]. Although leafy spurge abundance was reduced substantially after 20 years of annual herbicide treatments at Devil's Tower National Monument in Wyoming, populations were not eradicated. Researchers suggested that preventing population spread would require continuing spot herbicide treatments indefinitely [17]. A single herbicide treatment in a leafy spurge-infested grassland near Grass Range, Montana, was associated with long-term decreases in some native forbs and likely an increased abundance of leafy spurge. Prairie goldenrod (*Solidago missouriensis*) and western yarrow (*Achillea millefolium*) did not recover to pretreatment population levels even 16 years after the herbicide application, regardless of posttreatment grazing. Velvety goldenrod (*S. mollis*), white prairie aster (*Symphyotrichum falcatum*), American vetch (*Vicia americana*), and fringed sagebrush (*Artemisia frigida*) were significantly rarer after the herbicide treatment when plots were not grazed. Researchers concluded that when managing nonnative, invasive species, "the treatment can be worse than the disease" [185].

Several studies report that chemical control of leafy spurge, especially large populations, is often cost prohibitive [117]. A rancher in central Montana spent $25,000 over 2 seasons to apply herbicides to leafy spurge and described treatment results as like having "put fertilizer on the stuff" (Elliot 1997 cited in [41]). In a weed management review, Fay [53] reports that "eradication of well established leafy spurge patches with herbicides is nearly impossible. The picloram rates needed for control (of leafy spurge) are four to eight times the rates used for spotted knapweed" (*Centaurea maculosa*), making large population treatments extremely costly. Based on rangeland condition factors including grazing values, carrying capacities, leafy spurge spread rates, herbicide effectiveness, and treatment costs, researchers reported that "the levels of productivity at which most herbicide treatment programs break even is higher than the levels of productivity found in much of North Dakota's grazing land" [9]. Lym and Messersmith [121] provide more information about the costs associated with chemical treatment of leafy spurge.

While herbicides are often effective in gaining initial control of a new invasion or a severe infestation, they are rarely a complete or long-term solution to weed management [28]. Some studies report improved control or herbicide effectiveness when chemical treatments were combined with other control methods; however, long-term control was rarely evaluated. In North Dakota's Little Missouri National Grassland, leafy spurge was reduced at least initially when a fall herbicide treatment was followed by a spring fire [83]. Along rights of way in Eden Prairie, Minnesota, leafy spurge was nearly eliminated after sites were twice treated with herbicides followed by fall fires. Treated sites were dominated by yellow foxtail (*Setaria pumila* subsp. *pumila*) and witchgrass (*Panicum capillare*) immediately following 2 years of treatments [18]. In North Dakota grasslands, control of leafy spurge was better on plots treated with herbicide and biocontrols or herbicide and grass seeding than on plots treated with herbicide alone. Survival and growth of flea beetles could likely be improved by releasing them 1 year after herbicide treatments or releasing them in a refuge near the treated area [88]. For more on combining control methods to manage leafy spurge, see Integrated management below.

Integrated management: Several studies evaluated leafy spurge control using herbicides and/or fire together with biocontrols or posttreatment grass seeding. Combining goat grazing and herbicide treatments or herbicides and grass seeding often provided better control than either treatment alone; however, using herbicides with insect biocontrols rarely improved long-term leafy spurge control.

Biocontrols and herbicides: In North Dakota's Sheyenne National Grassland, goat grazing followed by a fall herbicide treatment reduced leafy spurge density more quickly and provided longer control than either method alone. However, several years after the treatments, differences between single and combination treatments were not always significant ($P<0.05$) [124]. Leafy spurge stem densities were reduced more rapidly when herbicides were used on sites with established flea beetle populations, but once flea beetles populations were established for 5 to 12 years, leafy spurge stems densities were rarely significantly different between herbicide-treated or untreated plots [123]. Findings were similar in leafy spurge-infested silver sagebrush-grasslands in Theodore Roosevelt National Park, North Dakota. Within 3 years of herbicide treatment, density of leafy spurge stems was not significantly different on flea beetle sites with and without herbicide treatment. The herbicide-treated plots, however, did have significantly fewer flea beetles than untreated plots 1 and 2 years later ($P<0.05$) [106].

Herbicides and/or fire and grass seeding: Several studies suggest that herbicide application and/or burning followed by grass seeding can provide leafy spurge control, which may persist for several years. An herbicide treatment followed by seeding of brome (*Bromus* spp.), wheatgrass (*Agropyron* spp.), or wildrye (*Elymus* spp.) cultivars often reduced leafy spurge stem densities [125]. Seven to 10 years following an herbicide treatment and no-till seeding of wildrye and wheatgrass in Crook County, Wyoming, leafy spurge cover was at least 20% lower than on control plots [55]. On a floodplain in the Minnesota Valley National Wildlife Refuge, 2 years after plots were herbicide treated and seeded with little bluestem or mixed grasses, leafy spurge cover was significantly reduced from pretreatment levels ($P<0.05$). On plots treated only with herbicides, control of leafy spurge was noted for only 1 year [16].

Leafy spurge was controlled in mixed-grass prairie sites in Nebraska, at least temporarily, after native grasses or grass-legume mixes were seeded on sites prepared through a combination of mowing, burning, and/or herbicide treatments. Leafy spurge abundance was lower and forage abundance was higher in treated than untreated plots. Long-term control of leafy spurge was not evaluated [134,135]. For additional information on controlling leafy spurge through the integrated use of herbicides, fire, and revegetation, see Masters and others [136].

APPENDIX: FIRE REGIME TABLE

SPECIES: Euphorbia esula

The following table provides fire regime information that may be relevant to leafy spurge habitats. Follow the links in the table to documents that provide more detailed information on these fire regimes.

Fire regime information on vegetation communities in which leafy spurge may occur. This information is taken from the LANDFIRE Rapid Assessment Vegetation Models [102], which were developed by local experts using available literature, local data, and/or expert opinion. This table summarizes fire regime characteristics for each plant community listed. The PDF file linked from each plant community name describes the model and synthesizes the knowledge available on vegetation composition, structure, and dynamics in that community. Cells are blank where information is not available in the Rapid Assessment Vegetation Model.

Pacific Northwest	California	Southwest
Great Basin	Northern and Central Rockies	Northern Great Plains
Great Lakes	Northeast	Southern Appalachians

Pacific Northwest

- Northwest Grassland
- Northwest Shrubland
- Northwest Woodland
- Northwest Forested

Vegetation Community (Potential Natural Vegetation Group)	Fire severity*	Fire regime characteristics			
		Percent of fires	Mean interval (years)	Minimum interval (years)	Maximum interval (years)
Northwest Grassland					
Bluebunch wheatgrass	Replacement	47%	18	5	20
	Mixed	53%	16	5	20
Idaho fescue grasslands	Replacement	76%	40		
	Mixed	24%	125		
Northwest Shrubland					
Wyoming big sagebrush semidesert	Replacement	86%	200	30	200
	Mixed	9%	>1,000	20	
	Surface or low	5%	>1,000	20	
Wyoming sagebrush steppe	Replacement	89%	92	30	120
	Mixed	11%	714	120	
Low sagebrush	Replacement	41%	180		
	Mixed	59%	125		
Mountain big sagebrush (cool sagebrush)	Replacement	100%	20	10	40
Northwest Woodland					
Oregon white oak-ponderosa pine	Replacement	16%	125	100	300
	Mixed	2%	900	50	
	Surface or low	81%	25	5	30
Ponderosa pine	Replacement	5%	200		
	Mixed	17%	60		
	Surface or low	78%	13		
Oregon white oak	Replacement	3%	275		
	Mixed	19%	50		
	Surface or low	78%	12.5		
Northwest Forested					
Douglas-fir (Willamette Valley foothills)	Replacement	18%	150	100	400
	Mixed	29%	90	40	150
	Surface or				

	low	53%	50	20	80
Ponderosa pine (xeric)	Replacement	37%	130		
	Mixed	48%	100		
	Surface or low	16%	300		
Dry ponderosa pine (mesic)	Replacement	5%	125		
	Mixed	13%	50		
	Surface or low	82%	8		
Mixed conifer (southwestern Oregon)	Replacement	4%	400		
	Mixed	29%	50		
	Surface or low	67%	22		
California mixed evergreen (northern California)	Replacement	6%	150	100	200
	Mixed	29%	33	15	50
	Surface or low	64%	15	5	30
Mixed conifer (eastside dry)	Replacement	14%	115	70	200
	Mixed	21%	75	70	175
	Surface or low	64%	25	20	25
Mixed conifer (eastside mesic)	Replacement	35%	200		
	Mixed	47%	150		
	Surface or low	18%	400		

California

- California Grassland
- California Shrubland
- California Woodland
- California Forested

Vegetation Community (Potential Natural Vegetation Group)	Fire severity*	Fire regime characteristics			
		Percent of fires	Mean interval (years)	Minimum interval (years)	Maximum interval (years)
California Grassland					
California grassland	Replacement	100%	2	1	3
Herbaceous wetland	Replacement	70%	15		
	Mixed	30%	35		

California Shrubland					
Coastal sage scrub	Replacement	100%	50	20	150
Coastal sage scrub-coastal prairie	Replacement	8%	40	8	900
	Mixed	31%	10	1	900
	Surface or low	62%	5	1	6
California Woodland					
California oak woodlands	Replacement	8%	120		
	Mixed	2%	500		
	Surface or low	91%	10		
Ponderosa pine	Replacement	5%	200		
	Mixed	17%	60		
	Surface or low	78%	13		
California Forested					
California mixed evergreen	Replacement	10%	140	65	700
	Mixed	58%	25	10	33
	Surface or low	32%	45	7	
Mixed conifer (North Slopes)	Replacement	5%	250		
	Mixed	7%	200		
	Surface or low	88%	15	10	40
Mixed conifer (South Slopes)	Replacement	4%	200		
	Mixed	16%	50		
	Surface or low	80%	10		
Aspen with conifer	Replacement	24%	155	50	300
	Mixed	15%	240		
	Surface or low	61%	60		
Jeffrey pine	Replacement	9%	250		
	Mixed	17%	130		
	Surface or low	74%	30		
Southwest					

- Southwest Grassland
- Southwest Shrubland
- Southwest Woodland
- Southwest Forested

Vegetation Community (Potential Natural Vegetation Group)	Fire severity*	Fire regime characteristics			
		Percent of fires	Mean interval (years)	Minimum interval (years)	Maximum interval (years)
Southwest Grassland					
Desert grassland	Replacement	85%	12		
	Surface or low	15%	67		
Desert grassland with shrubs and trees	Replacement	85%	12		
	Mixed	15%	70		
Shortgrass prairie	Replacement	87%	12	2	35
	Mixed	13%	80		
Shortgrass prairie with shrubs	Replacement	80%	15	2	35
	Mixed	20%	60		
Shortgrass prairie with trees	Replacement	80%	15	2	35
	Mixed	20%	60		
Montane and subalpine grasslands	Replacement	55%	18	10	100
	Surface or low	45%	22		
Montane and subalpine grasslands with shrubs or trees	Replacement	30%	70	10	100
	Surface or low	70%	30		
Southwest Shrubland					
Low sagebrush shrubland	Replacement	100%	125	60	150
Mountain sagebrush (cool sage)	Replacement	75%	100		
	Mixed	25%	300		
Southwest Woodland					
Pinyon-juniper (mixed fire regime)	Replacement	29%	430		
	Mixed	65%	192		
	Surface or low	6%	>1,000		

Ponderosa pine/grassland (Southwest)	Replacement	3%	300		
	Surface or low	97%	10		
Southwest Forested					
Riparian forest with conifers	Replacement	100%	435	300	550
Riparian deciduous woodland	Replacement	50%	110	15	200
	Mixed	20%	275	25	
	Surface or low	30%	180	10	
Ponderosa pine-Gambel oak (southern Rockies and Southwest)	Replacement	8%	300		
	Surface or low	92%	25	10	30
Ponderosa pine-Douglas-fir (southern Rockies)	Replacement	15%	460		
	Mixed	43%	160		
	Surface or low	43%	160		
Southwest mixed conifer (warm, dry with aspen)	Replacement	7%	300		
	Mixed	13%	150	80	200
	Surface or low	80%	25	2	70
Southwest mixed conifer (cool, moist with aspen)	Replacement	29%	200	80	200
	Mixed	35%	165	35	
	Surface or low	36%	160	10	
Aspen with spruce-fir	Replacement	38%	75	40	90
	Mixed	38%	75	40	
	Surface or low	23%	125	30	250
Stable aspen without conifers	Replacement	81%	150	50	300
	Surface or low	19%	650	600	>1,000

Great Basin

- Great Basin Grassland
- Great Basin Shrubland
- Great Basin Woodland
- Great Basin Forested

Vegetation Community (Potential Natural Vegetation Group)	Fire severity*	Fire regime characteristics			
		Percent of fires	Mean interval (years)	Minimum interval (years)	Maximum interval (years)

Great Basin Grassland					
Great Basin grassland	Replacement	33%	75	40	110
	Mixed	67%	37	20	54
Mountain meadow (mesic to dry)	Replacement	66%	31	15	45
	Mixed	34%	59	30	90
Great Basin Shrubland					
Basin big sagebrush	Replacement	80%	50	10	100
	Mixed	20%	200	50	300
Wyoming big sagebrush semidesert	Replacement	86%	200	30	200
	Mixed	9%	>1,000	20	>1,000
	Surface or low	5%	>1,000	20	>1,000
Wyoming big sagebrush semidesert with trees	Replacement	84%	137	30	200
	Mixed	11%	≥1,000	20	>1,000
	Surface or low	5%	>1,000	20	>1,000
Wyoming sagebrush steppe	Replacement	89%	92	30	120
	Mixed	11%	714	120	
Mountain big sagebrush	Replacement	100%	48	15	100
Mountain big sagebrush with conifers	Replacement	100%	49	15	100
Mountain sagebrush (cool sage)	Replacement	75%	100		
	Mixed	25%	300		
Mountain shrubland with trees	Replacement	22%	105	100	200
	Mixed	78%	29	25	100
Great Basin Woodland					
Juniper and pinyon-juniper steppe woodland	Replacement	20%	333	100	≥1,000
	Mixed	31%	217	100	≥1,000
	Surface or low	49%	135	100	
Ponderosa pine	Replacement	5%	200		
	Mixed	17%	60		
	Surface or	78%	13		

	Surface or low				
Great Basin Forested					
Interior ponderosa pine	Replacement	5%	161		800
	Mixed	10%	80	50	80
	Surface or low	86%	9	8	10
Ponderosa pine-Douglas-fir	Replacement	10%	250		≥1,000
	Mixed	51%	50	50	130
	Surface or low	39%	65	15	
Great Basin Douglas-fir (dry)	Replacement	12%	90		600
	Mixed	14%	76	45	
	Surface or low	75%	14	10	50
Aspen with conifer (low to midelevation)	Replacement	53%	61	20	
	Mixed	24%	137	10	
	Surface or low	23%	143	10	
Douglas-fir (warm mesic interior)	Replacement	28%	170	80	400
	Mixed	72%	65	50	250
Aspen with conifer (high elevation)	Replacement	47%	76	40	
	Mixed	18%	196	10	
	Surface or low	35%	100	10	
Stable aspen-cottonwood, no conifers	Replacement	31%	96	50	300
	Surface or low	69%	44	20	60
Stable aspen without conifers	Replacement	81%	150	50	300
	Surface or low	19%	650	600	>1,000

Northern and Central Rockies

- Northern and Central Rockies Grassland
- Northern and Central Rockies Shrubland
- Northern and Central Rockies Forested

Vegetation Community (Potential Natural Vegetation Group)	Fire severity*	Fire regime characteristics			
		Percent of fires	Mean interval (years)	Minimum interval (years)	Maximum interval (years)
Northern and Central Rockies Grassland					
	Replacement	55%	22	2	40

Northern prairie grassland	Mixed	45%	27	10	50
Mountain grassland	Replacement	60%	20	10	
	Mixed	40%	30		
Northern and Central Rockies Shrubland					
Riparian (Wyoming)	Mixed	100%	100	25	500
Wyoming big sagebrush	Replacement	63%	145	80	240
	Mixed	37%	250		
Basin big sagebrush	Replacement	60%	100	10	150
	Mixed	40%	150		
Low sagebrush shrubland	Replacement	100%	125	60	150
Mountain shrub, nonsagebrush	Replacement	80%	100	20	150
	Mixed	20%	400		
Mountain big sagebrush steppe and shrubland	Replacement	100%	70	30	200
Northern and Central Rockies Forested					
Ponderosa pine (Northern Great Plains)	Replacement	5%	300		
	Mixed	20%	75		
	Surface or low	75%	20	10	40
Ponderosa pine (Northern and Central Rockies)	Replacement	4%	300	100	≥1,000
	Mixed	19%	60	50	200
	Surface or low	77%	15	3	30
Ponderosa pine (Black Hills, low elevation)	Replacement	7%	300	200	400
	Mixed	21%	100	50	400
	Surface or low	71%	30	5	50
Ponderosa pine (Black Hills, high elevation)	Replacement	12%	300		
	Mixed	18%	200		
	Surface or low	71%	50		
Ponderosa pine-Douglas-fir	Replacement	10%	250		≥1,000
	Mixed	51%	50	50	130
	Surface or				

	low	39%	65	15	
Douglas-fir (xeric interior)	Replacement	12%	165	100	300
	Mixed	19%	100	30	100
	Surface or low	69%	28	15	40
Douglas-fir (warm mesic interior)	Replacement	28%	170	80	400
	Mixed	72%	65	50	250
Douglas-fir (cold)	Replacement	31%	145	75	250
	Mixed	69%	65	35	150
Lower subalpine lodgepole pine	Replacement	73%	170	50	200
	Mixed	27%	450	40	500
Lower subalpine (Wyoming and Central Rockies)	Replacement	100%	175	30	300

Northern Great Plains

- Northern Plains Grassland
- Northern Plains Woodland

Vegetation Community (Potential Natural Vegetation Group)	Fire severity*	Fire regime characteristics			
		Percent of fires	Mean interval (years)	Minimum interval (years)	Maximum interval (years)
Northern Plains Grassland					
Nebraska Sandhills prairie	Replacement	58%	11	2	20
	Mixed	32%	20		
	Surface or low	10%	67		
Northern mixed-grass prairie	Replacement	67%	15	8	25
	Mixed	33%	30	15	35
Southern mixed-grass prairie	Replacement	100%	9	1	10
Central tallgrass prairie	Replacement	75%	5	3	5
	Mixed	11%	34	1	100
	Surface or low	13%	28	1	50
Northern tallgrass prairie	Replacement	90%	6.5	1	25
	Mixed	9%	63		
	Surface or				

	low	2%	303		
Southern tallgrass prairie (East)	Replacement	96%	4	1	10
	Mixed	1%	277		
	Surface or low	3%	135		
Oak savanna	Replacement	7%	44		
	Mixed	17%	18		
	Surface or low	76%	4		
Northern Plains Woodland					
Oak woodland	Replacement	2%	450		
	Surface or low	98%	7.5		
Northern Great Plains wooded draws and ravines	Replacement	38%	45	30	100
	Mixed	18%	94		
	Surface or low	43%	40	10	
Great Plains floodplain	Replacement	100%	500		

Great Lakes

- Great Lakes Grassland
- Great Lakes Woodland
- Great Lakes Forested

Vegetation Community (Potential Natural Vegetation Group)	Fire severity*	Fire regime characteristics			
		Percent of fires	Mean interval (years)	Minimum interval (years)	Maximum interval (years)
Great Lakes Grassland					
Mosaic of bluestem prairie and oak-hickory	Replacement	79%	5	1	8
	Mixed	2%	260		
	Surface or low	20%	2		33
Great Lakes Woodland					
Great Lakes pine barrens	Replacement	8%	41	10	80
	Mixed	9%	36	10	80
	Surface or low	83%	4	1	20
Jack pine-open lands (frequent fire-return	Replacement	83%	26	10	100

interval)	Mixed	17%	125	10	
Northern oak savanna	Replacement	4%	110	50	500
	Mixed	9%	50	15	150
	Surface or low	87%	5	1	20
Great Lakes Forested					
Conifer lowland (embedded in fire-prone system)	Replacement	45%	120	90	220
	Mixed	55%	100		
Conifer lowland (embedded in fire-resistant ecosystem)	Replacement	36%	540	220	≥1,000
	Mixed	64%	300		
Great Lakes floodplain forest	Mixed	7%	833		
	Surface or low	93%	61		
Great Lakes pine forest, jack pine	Replacement	67%	50		
	Mixed	23%	143		
	Surface or low	10%	333		
Maple-basswood	Replacement	33%	≥1,000		
	Surface or low	67%	500		
Maple-basswood mesic hardwood forest (Great Lakes)	Replacement	100%	>1,000	≥1,000	>1,000
Maple-basswood-oak-aspen	Replacement	4%	769		
	Mixed	7%	476		
	Surface or low	89%	35		
Oak-hickory	Replacement	13%	66	1	
	Mixed	11%	77	5	
	Surface or low	76%	11	2	25
Pine-oak	Replacement	19%	357		
	Surface or low	81%	85		
Red pine-eastern white pine (frequent fire)	Replacement	38%	56		
	Mixed	36%	60		
	Surface or low	26%	84		
	Replacement	30%	166		
	Mixed	47%	105		

Red pine-eastern white pine (less frequent fire)					
	Surface or low	23%	220		
Great Lakes pine forest, eastern white pine-eastern hemlock (frequent fire)	Replacement	52%	260		
	Mixed	12%	>1,000		
	Surface or low	35%	385		
Eastern white pine-eastern hemlock	Replacement	54%	370		
	Mixed	12%	>1,000		
	Surface or low	34%	588		

Northeast

- Northeast Woodland
- Northeast Forested

Vegetation Community (Potential Natural Vegetation Group)	Fire severity*	Fire regime characteristics			
		Percent of fires	Mean interval (years)	Minimum interval (years)	Maximum interval (years)
Northeast Woodland					
Eastern woodland mosaic	Replacement	2%	200	100	300
	Mixed	9%	40	20	60
	Surface or low	89%	4	1	7
Rocky outcrop pine (Northeast)	Replacement	16%	128		
	Mixed	32%	65		
	Surface or low	52%	40		
Pine barrens	Replacement	10%	78		
	Mixed	25%	32		
	Surface or low	65%	12		
Oak-pine (eastern dry-xeric)	Replacement	4%	185		
	Mixed	7%	110		
	Surface or low	90%	8		
Northeast Forested					
Northern hardwoods (Northeast)	Replacement	39%	≥1,000		
	Mixed	61%	650		
Eastern white pine-northern hardwoods	Replacement	72%	475		
	Surface or				

	low	28%	>1,000		
[Appalachian oak forest (dry-mesic)]	Replacement	2%	625	500	≥1,000
	Mixed	6%	250	200	500
	Surface or low	92%	15	7	26

Southern Appalachians

- Southern Appalachians Grassland
- Southern Appalachians Woodland
- Southern Appalachians Forested

Vegetation Community (Potential Natural Vegetation Group)	Fire severity*	Fire regime characteristics			
		Percent of fires	Mean interval (years)	Minimum interval (years)	Maximum interval (years)
Southern Appalachians Grassland					
Bluestem-oak barrens	Replacement	46%	15		
	Mixed	10%	69		
	Surface or low	44%	16		
Eastern prairie-woodland mosaic	Replacement	50%	10		
	Mixed	1%	900		
	Surface or low	50%	10		
Southern Appalachians Woodland					
Appalachian shortleaf pine	Replacement	4%	125		
	Mixed	4%	155		
	Surface or low	92%	6		
Table Mountain-pitch pine	Replacement	5%	100		
	Mixed	3%	160		
	Surface or low	92%	5		
Oak-ash woodland	Replacement	23%	119		
	Mixed	28%	95		
	Surface or low	49%	55		
Southern Appalachians Forested					
Oak (eastern dry-xeric)	Replacement	6%	128	50	100
	Mixed	16%	50	20	30
	Surface or	78%	10	1	10

	low				
Appalachian Virginia pine	Replacement	20%	110	25	125
	Mixed	15%	145		
	Surface or low	64%	35	10	40
Appalachian oak forest (dry-mesic)	Replacement	6%	220		
	Mixed	15%	90		
	Surface or low	79%	17		

*Fire Severities—
Replacement: Any fire that causes greater than 75% top removal of a vegetation-fuel type, resulting in general replacement of existing vegetation; may or may not cause a lethal effect on the plants.
Mixed: Any fire burning more than 5% of an area that does not qualify as a replacement, surface, or low-severity fire; includes mosaic and other fires that are intermediate in effects.
Surface or low: Any fire that causes less than 25% upper layer replacement and/or removal in a vegetation-fuel class but burns 5% or more of the area [62,101].

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