

#### Fire Effects Information System (FEIS)

# Centaurea stoebe subsp. micranthos, spotted knapweed

2021

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Figure 1—Flowering spotted knapweed in Bellevue Park, Sault Ste. Marie, Ontario.

Photo by Rob Routledge, Sault College, and courtesy of Budwood.org.

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## **SUMMARY**

This review summarizes the information that was available in the scientific literature as of 2021 on the biology, ecology, and effects of fire and control methods on spotted knapweed in North America.

Spotted knapweed is a nonnative, invasive forb in parts of the United States. It can occur in dense monocultures that displace native plants; reduce native plant and animal diversity; reduce native wildlife habitat and forage; alter soil physical and chemical properties; and increase surface water runoff and stream sedimentation. It is most invasive in grasslands, semi-arid shrublands, woodlands, and open forests. It is especially invasive after disturbance, so limiting disturbance may help prevent spotted knapweed invasion.

Spotted knapweed regenerates primarily from seed. Plants are also able to extend lateral shoots below the soil surface that form rosettes adjacent to the parent plant. It is a perennial or biennial, but sometimes behaves as an annual. Spotted knapweed seeds germinate throughout the growing season whenever moisture and temperature are suitable. Seedlings develop into rosettes with a taproot. Plants bolt then flower, typically between June and October, depending on location.

Spotted knapweed plants can produce hundreds or thousands of seeds. Seeds are typically dispersed short distances by gravity and wind. Seeds are also spread by animals, water, and vehicles. Spotted knapweed has a large, persistent soil seed bank. Viability of seeds in the soil seed bank is typically low, but some seeds may remain viable in the soil for up to 8 years. Spotted knapweed seeds germinate and seedlings establish best on moist, disturbed soils. However, seeds can germinate under a wide range of conditions and over an extended period. Once established, spotted knapweed can form monotypic stands on some sites.

Most information about spotted knapweed's response to fire comes from field studies using prescribed and experimental fires—alone and in combination with other methods—to control invasive populations of spotted knapweed. Most studies about spotted knapweed's response to fire were conducted in forests, tallgrass prairies, and other warm-season grasslands. Severe fire can kill spotted knapweed plants, but low-severity fire that does not damage the root crown is unlikely to kill them. If low-severity fire occurs prior to bolting, spotted knapweed plants are likely to sprout and produce flowering stems in the same growing season. Fires are usually not severe enough to kill spotted knapweed seeds in the soil seed bank, and spotted knapweed can reestablish from surviving seeds. Burning generally reduces spotted knapweed germination and seedling emergence, but fire is likely to create conditions that are favorable for spotted knapweed seedling establishment. Consecutive annual prescribed fires (or some other follow-up treatments) are then needed to prevent subsequent seed production and thus reduce spotted knapweed populations in the long term.

In addition to fire, physical and mechanical control, livestock grazing, biological control, and/or chemical control methods may be used in an integrated management program to control spotted knapweed. No matter what method is used to kill spotted knapweed plants, establishment or maintenance of desirable plants is needed for long-term control.

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## INTRODUCTION

#### FEIS Abbreviation CENSTOM

#### **Common Name**

spotted knapweed bushy knapweed spotted star-thistle

#### <u>Taxonomy</u>

The scientific name of spotted knapweed is *Centaurea stoebe* L. subsp. *micranthos* (Gugler) Hayek (Asteraceae) [21,141,172,234,344,512,526,532,551]. The *Centaurea stoebe* species complex consists of three subspecies: C. stoebe subsp. *micranthos*, C. stoebe subsp. stoebe, and C. stoebe subsp. serbica [344]. The native range of *C. stoebe* subsp. *micranthos* and *C. stoebe* subsp. *stoebe* is across Europe and western Asia, while the native range of *C. stoebe* subsp. *serbica* is limited to the Balkan Peninsula [344]. North American populations of spotted knapweed are almost entirely *C. stoebe* subsp. *micranthos*, and this subspecies is the only spotted knapweed subspecies considered invasive in North America

[<u>170,196,328,418</u>]. Therefore, studies in North America on invasive spotted knapweed pertain to *C. stoebe* subsp. *micranthos* in this review.

While both *C. stoebe* subsp. *micranthos* and *C. stoebe* subsp. *stoebe* appear to have been introduced to North America, *C. stoebe* subsp. *micranthos* was a more successful invader than *C. stoebe* subsp. *stoebe* [503]. The two subspecies overlap in many morphological traits [344,452], but differ in that *C. stoebe* subsp. *micranthos* is tetraploid and tends to be perennial and <u>polycarpic</u> while *C. stoebe* subsp. *stoebe* is diploid and tends to be biennial and <u>monocarpic</u> [170]. Invasion success of *C. stoebe* subsp. *micranthos* in North America has been attributed to tetraploidy and life history traits that preadapted it to conditions in the invaded range [50,90,169,196,329,334,417,483,490] and allowed for local morphological and phenological post-introduction adaptations [168,169,170,196,329,406], among other factors (see Life History Traits).

A fertile hybrid between diploid *Centaurea stoebe* subsp. *stoebe* and diffuse knapweed, *Centaurea* × *psammogena* G. Gáyer [345], has been reported in at least seven states [345] including Washington, Oregon, Idaho, Montana, Wyoming, Colorado [34], and Michigan [519]. The hybrid was most likely introduced to North America with diffuse knapweed around 1900 [34] and occurs in diffuse knapweed sites but not in tetraploid *Centaurea stoebe* subsp. *micranthos* sites in North America [31,34]. The Flora of North America reports that spotted knapweed "readily hybridizes" with diffuse knapweed [141]. However, hybridization between spotted knapweed and diffuse knapweed is not likely to occur in North America, due to the near absence of *Centaurea stoebe* subsp. *stoebe* in North America. Hybridization occurs only between diploid *Centaurea stoebe* subsp. *stoebe* and diploid diffuse knapweed and not between other cytotype pairings. While diploid *Centaurea stoebe* subsp. *stoebe* is relatively absent in North America, its range overlaps with that of diploid diffuse knapweed in some locations in Europe [34].

Common names are used throughout this review. For scientific names of plants and animals and links to other FEIS Species Reviews, see <u>table A1</u> and <u>table A2</u>.

## <u>Synonyms</u>

Acosta maculosa (Lamarck) Holub. [<u>141,452,512,528,529</u>] Centaurea biebersteinii DC. [<u>80,113,172,194,273,344,512,551</u>] Centaurea maculosa Lam. (misapplied [<u>527</u>]) [<u>80,99,141,157,158,163,262,532</u>] Centaurea maculosa Lam. subsp. micranthos S.G. Gmel. ex Gugler [<u>194</u>] Centaurea micranthos [<u>344</u>]

## <u>Life Form</u>

Forb

## DISTRIBUTION AND PLANT COMMUNITIES

## **GENERAL DISTRIBUTION**

Spotted knapweed is native to eastern Europe and western Asia [344]. It is thought to have been introduced to North America multiple times [211,303], possibly as a contaminant in alfalfa seed and/or ship's ballast, in the late 1800s [286,344,412,413,438,551].

Spotted knapweed did not spread immediately after being introduced. The first records in North America indicate that it was introduced near Westford, Massachusetts, in 1884, and in Victoria, British Columbia, in 1893. Its distribution remained confined to a few populations for about 20 years in the East and 40 years in the West after initial introductions [44]. Thus, the invasion of spotted knapweed appears to have occurred in two phases along two separate invasion routes: one expanding from the East and one from the West. During the first phase, it spread into ruderal habitats similar to its native niche. During the second phase, it spread from ruderal habitats into natural and seminatural habitats that were less similar to its native niche [44,490] (see <u>Site Characteristics</u>). By 1980, spotted knapweed had spread to 48 counties in the Pacific Northwest. Between 1980 and 1998, spotted knapweed occurred in at least 326 counties in the West, including every county in Washington, Idaho, Montana, and Wyoming [438].

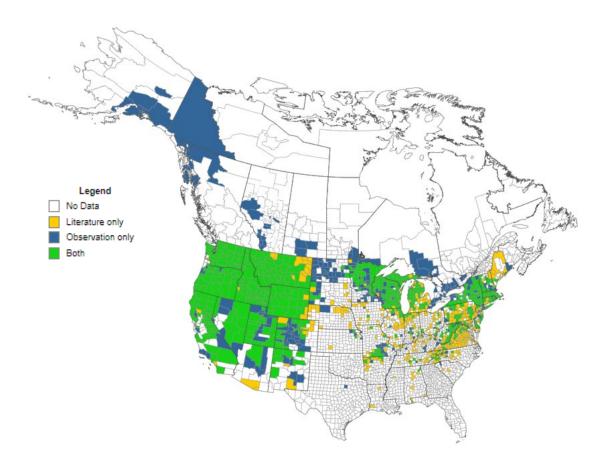


Figure 2—County-level distribution of spotted knapweed in the United States. Map courtesy of EDDMaps [127], accessed 2021 July 28.

In the United States, spotted knapweed occurs in as many as 49 states [127,233,512] and in Canada it occurs in as many as six provinces and one territory [127,512]. Although spotted knapweed is widespread in North America, it is found primarily in the western, midwestern, and northeastern states and southern Canadian provinces [127,233,512] (fig. 2). In the Great Plains, populations are small and isolated and may not persist in some areas [163,416]. In 2004, the "worst infested states" were Washington, Oregon, Idaho, and Montana [383]. Surveys of land managers suggested that spotted knapweed occurred on about 3.0 million ha across 16 western states and provinces in 2000 [122]. In

2003, it occurred on about 2.1 million ha in 17 western states and about 0.7 million ha in eastern states [<u>118,120</u>]. While these studies cover slightly different areas, they suggest that the area occupied by spotted knapweed decreased substantially over those 3 years. The reason for this difference in area occupied was not addressed by the authors; however, spotted knapweed population size fluctuates from year to year and with timing and amount of precipitation (see <u>Population Structure and Growth</u>), which may explain differences in estimates of area occupied.

## SITE CHARACTERISTICS

Spotted knapweed distribution and abundance appears to be most influenced by <u>climate</u>, <u>soils</u>, and <u>disturbance [5,87]</u>. It is most invasive in North America in disturbed sites where site characteristics match those found within its native range, but its climatic niche shifted during its North American invasion and it now invades disturbed and undisturbed sites that are both drier and wetter [44,46].

The initial spread of spotted knapweed in both the eastern and western invaded ranges in the United States occurred almost exclusively from ruderal habitats (open, disturbed habitats, including croplands, fields, and transportation corridors) to other ruderal habitats on sites similar to its native range. It then spread into adjacent natural and semi-natural habitats, expanding its niche. Colonization of natural and semi-natural habitats was faster in the East than the West. The fast spread in the East was attributed to the well-developed railroad network and the relatively uniform and similar climate in the East compared to the native range. The slow spread in the West was attributed to climate differences in the West compared to the native range. After the 1950s, spotted knapweed "suddenly colonized" new habitats in the West that were warmer and both wetter and drier than that of its native range due to postintroduction adaptations and niche limit expansions [44].

## **Climate**

The amount and timing of precipitation affects spotted knapweed <u>establishment</u> and <u>growth</u>. Spotted knapweed occurs in places with mean annual precipitation ranging from 200 to 2,0000 mm [7,87,259] (table 1), indicating a tolerance for a broad range of annual precipitation levels [82]. However, in Washington, Idaho, and Montana, the largest populations tend to occur on shallow or well-drained soils in locations with 250 to 350 mm of annual precipitation [87]. Of 116 spotted knapweed populations studied in Montana, most occurred in areas with 300 to 760 mm of annual precipitation [82]. In the Northeast, areas with low to moderate growing season precipitation averages, moderate minimum temperature, and high sand content had the highest probability of spotted knapweed presence. Spotted knapweed occurred predominantly in open, disturbed areas [5] (see <u>Succession</u>).

Location	Mean annual precipitation (mm)
Northwest, Interior Columbia River	240–2,000 [7]
Basin and the Upper Missouri River	
Basin	
Colorado, near Boulder	514–527 [ <u>394,427]</u>
Idaho	280–690 [ <u>173,309,365]</u>
Michigan	369–973 [ <u>201,306</u> ]
Minnesota, near Detroit Lakes	662 [ <u>114]</u>
Montana	200–2,000 [10,78,84,259,432,436,461,475,500,508]
New York, east-central	930 [ <u>143]</u>
Washington, Idaho, and Montana	200–2,000 [87]
Wisconsin, near Webster and	770–800 [ <u>114]</u>
Wautoma	
British Columbia, southern interior	251–648 [ <u>145,210,524</u> ]

<b>T</b>     <b>A</b>   <b>A</b>		
Table 1—Mean annual	precipitation in some areas	s where spotted knapweed occurs.

## **Topography**

Spotted knapweed grows at elevations as low as 30 m in southern interior British Columbia [524] and up to 3,040 m in Montana [259] (table 2), although it is less invasive at the highest elevations. In Montana, spotted knapweed is rare in subalpine and alpine zones [138,142,326]. Of 116 spotted knapweed populations studied in Montana, most occurred in areas from 1,200 to 1,500 m; only 14% of populations occurred at higher elevations [82]. In the Middle Rocky Mountains Ecoregion, alpine areas were classified as "uninvaded" by spotted knapweed, while subalpine and high-elevation sites were classified as "invasive with disturbance". In other mountainous ecoregions of Washington, Oregon, Idaho, and Montana, alpine, subalpine, and high-elevation sites were also categorized as "invasive with disturbance" [364]. See Succession for more information on spotted knapweed's response to disturbance.

Table 2 - Llevational range of spotted knapweed by location.					
Location	Elevation (m)				
United States					
Four Corners Region	1,645–2,590 [ <u>194]</u>				
Northwest, Interior Columbia River	450–2,460 [7]				
Basin and the Upper Missouri River					
Basin					
California	up to 2,600 [ <u>21,447,458]</u>				
Colorado, near Boulder	1,810–2,070 [ <u>248,288,427,546</u> ]				
Idaho, northern	661–1,519 [ <u>150,298]</u>				
Michigan, Pinckney	290 [ <u>298]</u>				
Michigan, along Lake Michigan	0–300 above mean water level [ <u>392</u> ]				
Minnesota, near Detroit Lakes	1,477–1,500 [ <u>114</u> ]				
Montana	578–3,040 [ <u>10,38,84,178,259,295,400,462,474,500</u> ]				
Nevada, south-central	1,676–1,768 [24]				
New York, east-central	60–120 [ <u>143</u> ]				
North Dakota, Devil's Lake	443 [ <u>298]</u>				

Table 2—Elevational range of spotted knapweed by location.

Oregon, The Dalles	100 [298]
Utah	1,615–2,565 [ <u>158,532</u> ]
Virginia, Shenandoah National Park	1,067 [ <u>397</u> ]
Washington	up to 2,073 [ <u>298,412,414]</u>
Washington, Idaho, and Montana	576–3,030 [ <u>87]</u>
Wisconsin, near Webster and	920–1,000 [114]
Wautoma	
Canada	
British Columbia, southern interior	30–1,200 [ <u>145,152,204,307,524</u> ]
Ontario, Guelph	334 [ <u>298]</u>

Spotted knapweed occurs in plains and valleys and on montane sites [262,273] on all aspects, but in Montana, it is especially common on steep, south-facing slopes [124,326,537]. For example, on the Bitterroot National Forest, spotted knapweed occurs in most forests on south-facing slopes with <40% tree cover and below 2,000 m [138]. Throughout its North American distribution, spotted knapweed occurs on slopes ranging from flat to steeply sloping (>60%) [22,87,124,175,204,220,248,443,445].

## <u>Soils</u>

**Soil depth, texture, and type**: Spotted knapweed does not appear to be limited by soil characteristics. It occurs commonly in both shallow and deep [<u>135,412</u>] soils with a range of textures [<u>87</u>] and types [<u>82,344</u>]. In Montana, Idaho, and Washington, spotted knapweed occurs in sand, loam, clay loam, silty loam, sandy loam, silty clay loam, and sandy clay loam soils [<u>87</u>]. However, spotted knapweed does especially well in coarse-textured soils [<u>176,315,412,414,415,537</u>] and may fail to establish in soils with high clay content [<u>407</u>]. For example, the spotted knapweed dominance type in Montana occurs in coarse-textured substrates that are sandy or gravelly, such as sand or gravel bars along rivers and streams [<u>176</u>]. Spotted knapweed has been described as best adapted to Montana rangelands with "light-textured" (e.g., sandy) soils that receive summer rainfall, while in northeastern Washington, it is "best suited" to glacial till and outwash soils [<u>412</u>]. In the Northeast, high sand content was one of the most influential predictors of spotted knapweed presence [<u>5</u>] (see <u>Climate</u>). In the Great Lakes region, spotted knapweed is invasive on sand dunes [<u>23,103,156,392</u>] (see <u>Impacts</u>).

**Soil moisture:** Spotted knapweed grows on dry to moist sites. It is most productive on well-drained soils with low water-holding capacity [87,101,105,179]. It does poorly where soils are saturated or flooded [182,435,524]. While found in wetlands and riparian areas [91,177], often colonizing gravel bars and areas disturbed by flooding [91,177,179,494] (see Plant Communities), spotted knapweed is considered an obligate [435] or facultative [176] upland species. In southwestern Montana, spotted knapweed seedling emergence and survival to the second growing season were greater in upland than wetland areas. In wetland areas, seedlings established only on high-elevation microsites and no seedlings survived to the second growing season [435]. In dry areas, spotted knapweed germinates and grows well on sites where summer precipitation is supplemented by run-off [182,412,438], such as along ditch banks [124] and in depressions [81].

Water use and water-use efficiency of spotted knapweed is similar to many associated native plants [<u>37</u>]. On semiarid steppe in southwestern Montana, spotted knapweed had similar water use efficiency as bluebunch wheatgrass, western wheatgrass, and smooth brome, except during unusually dry conditions. It maintained greater water potentials than the grasses despite greater transpiration.

Changes in soil water indicated uptake from deeper and wetter soils by spotted knapweed than by the grasses [203]. In a greenhouse study, spotted knapweed had similar water use and water-use efficiency as bluebunch wheatgrass, western wheatgrass, and Idaho fescue [37], and several studies found that spotted knapweed is a better competitor for soil water resources in the introduced range than the native range [13,66,479,482].

#### **PLANT COMMUNITIES**

Spotted knapweed is invasive in grasslands (particularly bunchgrass steppes, prairies, montane grasslands, riparian areas, wetland margins, old fields, rangelands, and pastures), semi-arid shrublands, woodlands, and open forests [91,99,101,178,262,273]. See <u>table A3</u> for a representative list of plant classifications in which spotted knapweed occurs.

#### **United States**

**Intermountain West and Rocky Mountains:** In the 2004 publication on the status and trends of sagebrush ecosystems, spotted knapweed was classified as "highly invasive" in bunchgrass communities, dogwood and willow shrub wetlands, black cottonwood communities, and herbaceous sedge-dominated wetlands [91]. It was classified as "moderately invasive" in basin big sagebrush, mountain big sagebrush, Wyoming big sagebrush, and threetip sagebrush communities [91] and a species of management concern in western juniper woodlands throughout the Intermountain West [91].

In Montana, spotted knapweed grows in nearly every habitat type west of the Continental Divide [326], although it is rare in subalpine and alpine communities [138,142,326] (see Topography). It is particularly invasive in foothill prairies and montane grasslands (previously dominated by bluebunch wheatgrass, Idaho fescue, rough fescue, and needle and thread) and in openings in adjacent ponderosa pine/Douglas-fir communities [84,138,142,318,319,330,402,412,413,520]. On National Forests in western Montana, spotted knapweed was most common in burned areas in Douglas-fir and ponderosa pine habitat types and not particularly invasive in burned subalpine fir habitat types [137,138].

Spotted knapweed is common on exposed gravel bars along rivers and streams in Montana, Idaho, and Colorado [<u>176,177,178,248,250</u>] and is listed as a "dominance type" on upper terraces of major river courses, relatively dry, disturbed sites, and gravel bars [<u>179</u>].

**Pacific Northwest:** In Washington, spotted knapweed is found in openings in ponderosa pine/bunchgrass or Douglas-fir/shrub forests, especially on coarse, gravelly glacial soils [414]. It is common in disturbed forests in northeastern Washington, including ponderosa pine and Douglas-fir communities [415]. In the Columbia River Gorge, spotted knapweed ranked second in cover and frequency was >50% in ravines in the central broadleaf forest association [545].

**Southwest:** Spotted knapweed is common on disturbed sites throughout the Southwest (e.g., [24,194,532]). In south-central Nevada, spotted knapweeds occurs in disturbed saltbush and sagebrush communities [24]. In southwestern ponderosa pine forests, spotted knapweed is considered a "high-priority species for control" due to its ability to expand into and persist in undisturbed forests [449]. In Arizona, spotted knapweed occurs in pinyon-juniper grasslands [136].

**Great Plains:** In the Great Plains, spotted knapweed occurs in prairies, pastures, fields, and disturbed areas such as roadsides [53,163,315]. It occurs along roadsides in Montana and North Dakota in shortgrass and mixedgrass prairies. It occurs in foothill grasslands and in ponderosa pine, Douglas-fir,

and subalpine fir forest types. Spotted knapweed tends to spread from disturbed roadsides and establish in less disturbed communities in the shortgrass, mixedgrass, and foothill grasslands [<u>315</u>].

**Midwest:** In the Upper Midwest, spotted knapweed occurs in old fields, undisturbed dry prairies, oak and pine barrens, rangelands, lake dunes, and sandy ridges [77,101,144,518]. In Michigan, spotted knapweed has invaded restored and remnant tallgrass prairies, oak woodlands, and jack pine barrens [2]. On sand dunes of the Midwest, spotted knapweed is considered "one of the most critical threats to the long-term viability" of sand dune thistle, a federally threatened species [23] (see Impacts on Native Plant Communities). In Missouri, spotted knapweed occurs along stream banks, margins of ponds and fens, and in sand prairies. It also occurs along transportation corridors and in old fields and pastures [551].

**East:** In the Northeast, spotted knapweed occurs along sandy or gravelly banks, on sand dunes, in fields, along railroads, and in open rights-of-way [157,172,321]. In the Appalachian Region and the Southeast, spotted knapweed is common in fields, pastures, roadsides, clearings, and disturbed areas [80,378,527]. In Virginia, it is occasionally invasive in dry, natural habitats, such as shale barrens [80].

## <u>Canada</u>

Spotted knapweed occurs in most Canadian provinces, but is especially invasive in native grasslands in southwestern Canada. In British Columbia, spotted knapweed occurs primarily in the Bunchgrass, Ponderosa Pine, and dry phases of the Interior Douglas-fir Biogeoclimatic Zones. Its range extends into the Interior Cedar-Hemlock and Montane Spruce Biogeoclimatic Zones, but typically only along forest roads and in cut forests [152,322,389]. Bluebunch wheatgrass communities in British Columbia are especially susceptible to spotted knapweed invasion [4]. In the Kootenay Region of British Columbia, spotted knapweed is invasive in needle and thread-bluegrass types with scattered ponderosa pine and Douglas-fir [322]. In Waterton Lakes National Park, Alberta, spotted knapweed is an invasive species of "highest priority of concern" due to its abundance and ability to rapidly colonize new areas following disturbance [346]. In the Saskatchewan Prairie Ecozone, spotted knapweed occurred with low cover (1%) in a recent alluvial bar community type dominated by balsam poplar, as well as mountain rush and reed canarygrass community types [494]

## **BOTANICAL AND ECOLOGICAL CHARACTERISTICS**

## **BOTANICAL DESCRIPTION**

This description covers characteristics that may be relevant to fire ecology and is not meant for identification. Identification keys are available (e.g., [21,99,157,163,172,194,262,273,527,532]).

North American floras typically describe spotted knapweed as a biennial and/or a perennial forb (e.g., [21,77,80,99,113,157,163,207,273,532]). The Flora of West Virginia describes spotted knapweed as an annual or a biennial [473], but an annual life cycle is rare [424]. In Montana, spotted knapweed is predominantly a perennial [38].



Figure 3—Flowering spotted knapweed plant. Photo by Joseph M. DiTomaso, University of California Davis, and courtesy of Bugwood.org.

During the juvenile stage, spotted knapweed is a basal rosette (hereafter, rosette) [101,438]. Basal leaves are borne on short stalks and grow up to 20 cm long and 5 cm wide [80,101,163,438], with margins divided into linear or oblong segments [80]. Beginning usually the second year, each spotted knapweed plant produces 1 to 6 but up to 20 flowering stems/plant [101,438]. Stems range from 0.2 to 1.8 m tall (e.g., [21,77,80,99,163,194,262,273,473,532]). Stem leaves are alternate and grow smaller near the tops of stems. Their uppermost leaves are small and simple [80,101,262,438]. Stems branch in their upper half [438,524,532,551].

Flowerheads terminate the numerous branches [77,99]. They are solitary or borne in clusters of two or three [438,524], and are purple to pinkish-purple, rarely white (e.g., [21,77,80,99,101,113,163,194,438,532]).

Seeds are achenes [<u>113,273</u>] or cypselae [<u>80,172,194</u>] that are typically 2.5 to 3.5 mm long [<u>75,80,113,163,194,438,551</u>], but up to 4 mm long [<u>273</u>]. Seeds usually have a pappus of uneven bristles that are typically 0.5 to 3.5 mm long [<u>21,77,99,157,163,194,438,532,551</u>], but may be up to 5 or 6 mm long [<u>80,172</u>].

Spotted knapweed has a deep, stout taproot [<u>113,163,194,262,438,551</u>]. In Corvallis, Montana, average taproot length exceeded 30 cm [<u>463</u>]. Taproot diameter increases with age until about 5 years old [<u>472</u>].

Some plants also produce fine, fibrous lateral roots. Roots are colonized by <u>arbuscular mycorrhizal fungi</u> (AMF) which may contribute to its invasiveness in some native grasslands (e.g., [<u>180,396</u>]).

## Plant Longevity

Spotted knapweed plants can live for at least 12 years. Plants >7 years old have high incidence of root rot, making it difficult to age old plants using root ring counts [38]. In western Montana, the average age of plants, excluding plants <1 year old, was about 3 years old at five sites during 1 year and about 5 years old at 6 sites the following year. The higher average age the following year was attributed to high mortality among young age classes due to July drought [38] (see <u>Plant Mortality</u>).

## Population Structure and Growth

Spotted knapweed may occur as solitary plants or small patches, especially where establishment is recent, but it can also form large, dense monotypic stands [207,437]. Density increases with the age of the population and the degree of disturbance [524]. Spotted knapweed density in North America can average 47 times higher than density in its native range (D. E. Pearson, Y. K. Ortega, and S. Sears, unpublished data cited in [369]) and spotted knapweed does not form monocultures in its native range [65].

Spotted knapweed populations largely expand through peripheral enlargement of existing stands [524]. During a period of population expansion in Ann Arbor, Michigan, the oldest plants were 4 to 5 years old and largely occurred in the central area of the stand, while the youngest plants occurred throughout but "grossly dominated" at the periphery of the stand and in a satellite patch. During a period when the population was "static", this spatial age structure was lost and the different age classes were homogenously distributed throughout the stand [109].

Population density can vary substantially from year to year, and generally increases with increasing precipitation (e.g., [475]). Spring and early summer precipitation may be particularly influential on spotted knapweed population density. In two areas at the Big Hole National Battlefield in southwestern Montana, the total number of spotted knapweed plants increased from 244 to 2,784 individuals in the study area over 3 consecutive years, a result attributed to several consecutive years of wet spring weather [475]. Drought often contributes to spotted knapweed population decline (e.g., [38,341,354,359,374]). At six sites in western Montana, the overall density of spotted knapweed declined by 40% between 1984, a year of average precipitation, and 1985, a year with summer drought [38]. Declines in spotted knapweed density in western Montana in the early 2000s were attributed to drought during June (e.g., [341,354,359,374]). Biological control insects may contribute to declines in spotted knapweed establishment and mortality. High spring precipitation appears to favor spotted knapweed seedling establishment [363], while seedling mortality may be high when conditions are dry following emergence [524] (see Seedling Establishment and Mortality).

Spotted knapweed population growth rates increase with disturbance that opens the canopy, increases space, bare soil, and available soil nutrients, and decreases competition with associated vegetation for resources [6]. Demographic models indicated that spotted knapweed population growth rates increased with disturbance (simulated with a weed whipper and a soil aerator) due to substantial increases in survival of rosettes and reproduction of plants on disturbed sites. The increased population growth rate occurred independent of spotted knapweed density [6].

#### **Raunkiaer Life Form**

Hemicryptophyte [393]

#### SEASONAL DEVELOPMENT

Spotted knapweed seeds germinate throughout the growing season when temperature and moisture are suitable [101] (see <u>Germination and Seedling Emergence</u>). In Montana and British Columbia, they typically germinate in spring [217,463]. In New York, they mostly germinate in fall but also in spring [321]. Seedlings then develop into rosettes [217,524].

Seedlings can develop into rosettes, bolt, and flower during the year of seedling emergence, but this is rare [424]. Seedlings can also develop into rosettes throughout the summer, overwinter, and bolt during the following year, but many plants can live as rosettes for many years before bolting [38,101,424,472]. For example, most spotted knapweed plants germinating in March (93%) and April (94%) from seeds sown onto tilled fields in Spokane, Washington, produced flowers during their second year, while plants germinating in June, July, or later, did not flower until their third year [424]. In an old field in Corvallis, Montana, fall germinated seedlings did not flower their first summer of growth. All bolted spotted knapweed plants were  $\geq 2$  years old, but only 10% of 2-year-old plants bolted [472]. In another study in Montana, the percentage of flowering plants peaked in 5-year-old plants during the first year of a study and 7-year-old-plants during the second year [38]. In New York, no spotted knapweed plants flowered in their first year, <6% flowered in their second year, 39% to 57% flowered in the third year, and "a few" had not yet flowered in their fourth year [321]. In a common garden study, the probability and time of bolting was dependent on rosette size in early July [332].

Flowering occurs from June through October, depending on location [438] (table 3). Although some locations in the Southeast may flower through November (table 3), and in Arkansas, spotted knapweed may bolt and flower in late fall and early winter, despite the lack of pollinators at that time [139]. Flowering date varies within as well as among locations. Within a 1,024-ha area dominated by spotted knapweed in Montana, spotted knapweed was growing in various phenological stages ranging from recent flowering to early senescence on a single day in August [268]. Individual flowers bloom for 2 to 6 days [101]. Bracts of the flowerheads open when dehydrated [438]. Spotted knapweed flowerheads that are not infested with biological control seedhead-feeding insect larvae (see <u>Biological Control</u>) open when the seeds are mature and the seedheads are dry [412]. Seeds usually mature from mid-August through mid-September in Montana [126,438] and in mid-August in southern interior British Columbia [524].

Most seeds are shed upon maturity; very few overwinter in seedheads [438,460]. At two sites near Bozeman, Montana, spotted knapweed seed dispersal occurred primarily during August and September, with 30% to 62% of the seeds produced reaching the soil surface by October [217]. In Missoula, Montana, seed dispersal occurred from September to November [375].

Location	Flowering months
Great Plains	July–September [ <u>163]</u>
Four Corners Region	June–October [ <u>194]</u>
Northeastern United States and	June–October [ <u>157</u> ]
adjacent Canada	
Southeastern and mid-Atlantic	late June–November [525,526]
states	
Upper Midwest	late June–September [ <u>101</u> ]
Arkansas	intermittent flowering: April–November; peak flowering: June–
	July [ <u>139]</u>
California	July–September [ <u>21</u> ]
Michigan	mid-June–mid-August; full bloom in July [ <u>154</u> ]
Montana	July–September [ <u>262,341,438,484]</u>
Nevada	August–September [24]
New York	July–September [ <u>255,321</u> ]
Tennessee	summer [ <u>80]</u>
Utah	July–August [ <u>158]</u>
Virginia	late June–November [ <u>80,308]</u>
West Virginia	July–August [ <u>473</u> ]
Wisconsin	June–October [77]; peak early to mid-August [518]
British Columbia, southern	July–August [ <u>524]</u>
interior	

Table 3—Flowering months in some areas where spotted knapweed occurs.

Rosettes that do not bolt typically die back to the root crown over winter [437]. Root crowns form rosettes in spring and may bolt in early May in Montana [438] and southern British Columbia [524]. However, in Arkansas, rosettes often remain green throughout the winter [139]. Spotted knapweed root crowns can extend lateral shoots below the soil surface that form rosettes adjacent to the parent plant. This typically occurs in early spring in southern British Columbia [524] (see <u>Vegetative Reproduction and Regeneration</u>).

Many spotted knapweed plants survive in a vegetative state after flowering; in a greenhouse, >90% survived after flowering [50], while in a field experiment, 35% to 78% survived after flowering [321]. Some plants may flower during 1 year and flower again the next year [321].

## **REGENERATION PROCESSES**

Spotted knapweed reproduces sexually and regenerates almost entirely from seed [462]. Plants are also able to extend lateral shoots below the soil surface that form rosettes adjacent to the parent plant [101,438,524]. The amount and timing of precipitation is particularly important to spotted knapweed regeneration processes. It affects spotted knapweed <u>seed production</u> [217,324,394,424,427,438,455], <u>seedling establishment [363], growth [94,376,455,472]</u>, and <u>survival [38,250,289,329,360]</u>, and alters population abundance [217,329,360,475].

## **Pollination and Breeding System**

Fertilization of spotted knapweed requires cross-pollination. This can limit the reproductive success of isolated individuals, but it also promotes genetic diversity and may thereby contribute to invasiveness

[<u>186</u>]. Fertilization of spotted knapweed requires cross-pollination between flowers on different plants (obligately xenogamous) [<u>186,511</u>].

Spotted knapweed is primarily insect pollinated [186,524]. Bees, especially honey bees and bumble bees, are important pollinators (e.g., [23,26,73,133,186,198,244,524]). One study found greenhouse-grown spotted knapweed plants did not set seed because of the absence of pollinators in the greenhouse [511]. For information on spotted knapweed use by and effects on pollinators, see <u>Arthropods</u>. High spotted knapweed pollen counts in late July and early August in the Missoula Valley, Montana, suggest that spotted knapweed is also wind pollinated [155].

## Seed Production and Predation

The number of seeds produced by an individual spotted knapweed plant or a population of spotted knapweed plants is highly variable among plants, sites, and years. A single seedhead can have as many as 37 seeds [424] and an individual plant may produce more than 25,000 seeds in a year [524]. A population of plants may produce nearly 64,000 seeds/m<sup>2</sup>/year [424], although most produce far fewer (table A4).

Spotted knapweed seed production varies with site conditions (available moisture, nutrient availability, and competition for these resources), seed predation, and herbivory. Site conditions and precipitation during the growing season probably have the greatest effect on the number of seeds produced each year, with more seeds produced on wet than dry sites [217] and during wet than dry years [324,394,424,427,438,455]. In southern interior British Columbia on an irrigated site, spotted knapweed produced an average of 25,260 seeds/plant, compared to about 680 seeds/plant on nonirrigated rangelands [524]. In Idaho, the number of viable seeds per flowerhead was less in dry years than in wet years [424]. Near Boulder, Colorado, seed production was higher with increased precipitation both in the presence ( $R^2 = 0.75$ , n = 13) and absence ( $R^2 = 0.44$ , n = 13) of biological control insects, although the increase in seed production was less with insects present than absent [394].

Greenhouse experiments suggest that 'stress factors' (e.g., competition and herbivory) can reduce spotted knapweed seed production. One study found that treatment (control, herbivory, herbivory + nutrient shortage, and herbivory + nutrient shortage + grass competition) affected physiology, morphology, growth, and size of plants and ultimately numbers of seeds produced, but did not result in substantial changes to the mass or quality of seeds and offspring produced. Plants grown in the most favorable environment (i.e., without grass competition, without herbivory, and with added nitrogen) produced, on average, 1,412 seeds/plant. Herbivory by two biological control insects reduced this to 730 seeds/plant. Herbivory in the absence of nitrogen fertilizer resulted in an average of 274 seeds/plant. Plants with all three stress factors (i.e., with grass competition, herbivory, and no added nitrogen) produced, on average, 117 seeds/plant [335,530]. Another study found that competition with meadow fescue in pots reduced spotted knapweed seed production, flowerhead mass, biomass, shoot number, and rosette survival [332,335].

Seed production can be greatly reduced (e.g., [<u>181,248,249,336,394,427,455,466,468,471</u>]) by biological control insect larvae that consume immature seeds and other tissues in spotted knapweed seedheads, but even with reductions by biological controls, spotted knapweed is still a prolific seed producer [<u>108,252,287,331,468</u>]. For example, near Boulder, Colorado, spotted knapweed seed production was negatively correlated with the presence of *Larinus minutus* (r = -0.305, n = 6,026) and *Urophora affinis* (r

= -0.152, n = 6,026), two seedhead-feeding insects. In their absence , seed production averaged 6.2 and 5.4 seeds/seedhead, respectively, compared with 3.1 and 3.9, respectively, in their presence [<u>394</u>]. However, root-boring biological control insect larvae (e.g., *Cyphocleaonus achates*) may not reduce seed production (e.g., [<u>93,360,404</u>]).

While biological control insects can reduce seed production of spotted knapweed, spotted knapweed recruitment does not appear to be seed limited in some populations ([455], Maddox 1982 cited in [374]) and reductions in seed density do not necessarily lead to reductions in spotted knapweed plant density (e.g., [331,336]) (see <u>Biological Control</u>). Shirman (1981) suggested that only about 0.1% of the seed produced under the conditions studied would be needed to maintain the size of the spotted knapweed stands observed [424]. Estimates of the minimum number of seeds needed each year for a spotted knapweed population to persist vary widely depending on site characteristics, from 11 to 1,000 [289], ~160 [471], 2,710 [250] and 38 ([250] using data from [299,300]) seeds/m<sup>2</sup>/year.

The effectiveness of biological control agents on limiting spotted knapweed seed production and reducing plant density are influenced by the assemblage of insect species and their interactions, the density of insects and length of establishment, plant resource availability (e.g., water availability and nitrogen), intra- and interspecific plant competition, and timing of management treatments (e.g., mowing date relative to spotted knapweed phenological stage) (e.g., [139,248,250,263,288,360,404,455,469,471]).

Many wildlife species consume spotted knapweed seeds. See <u>Importance to Wildlife and Livestock</u> for more information. See <u>Seed Dispersal</u> for information on seed viability after consumption by wildlife and livestock.

Methods of removing flowering stems, buds, flowers, and seedheads, such as prescribed fire [129,285], domestic sheep grazing [195,242,327,353], hand pulling [284], mowing [48,139,469], and clipping [28,365] can reduce spotted knapweed flowering, seed production, and density of seeds in the soil seed bank (see Fire as a Control Agent and Control). While spotted knapweed often forms new flowers after being defoliated [28,139,324,469], a single defoliation per year during the flowering or seed-producing stage is sufficient to reduce spotted knapweed seed production [28,327,408] because defoliation during the flowering or seed-producing stage is sufficiently late in the growing season that few, if any, viable seeds will be produced if spotted knapweed reflowers [28]. However, defoliation during the flower bud or bolting stages can result in the development of new flower buds that largely escape attack by seedhead-feeding insects and greater seed production than nondefoliated controls [139,469]. Defoliation after mature seed has been released does little to inhibit seed production [139,324]. Combining control methods, such as multiple biological control insects or biological control insects and properly timed domestic sheep grazing, may be even more effective at reducing seed production than either method alone [327,468,471].

## Seed Dispersal

As soon as bracts open, any movement of the stem (e.g., by wind or passing animals) expels the loosely held seeds from the head [438,524]. Because few seeds are held over winter, little after-ripening occurs in the capitula [342] (see <u>Germination and Seedling Emergence</u>). Spotted knapweed seeds have both a pappus and an elaiosome (fleshy seed structures rich in lipids and proteins adapted for animal dispersal) [399]. However, given the weight and high falling velocities of spotted knapweed seeds, long-distance

wind dispersal is "very unlikely" [169] and most seeds disperse <1 m from their parent plant [101,260,438,524]. Spotted knapweed populations spread outward and downwind from the perimeter of existing stands [260,412,438,524].

Animals facilitate long distance dispersal of spotted knapweed. Both domestic sheep and mule deer excrete viable seeds of spotted knapweed in their feces for 7 to 10 days after consumption, respectively [521]. Near Hamilton, Montana, great horned owls acted as indirect dispersers of spotted knapweed seeds. Great horned owl pellets contained spotted knapweed seeds, apparently resulting from the owls preying upon North American deermice. Only 1% of seeds germinated, indicating that some spotted knapweed seeds can be viable after being ingested by both species [377]. In two Palouse Prairie sites near Missoula, Montana, native ants selected and dispersed spotted knapweed seeds, while leaving native seeds, possibly because spotted knapweed seeds have elaiosomes and native species do not [229].

Seeds mixed with soil and mud may be carried by vehicles or other equipment that, in turn, create an ideal seedbed for spotted knapweed establishment [412,438,524]. Seed dispersal by vehicles along roads and railways facilitate spotted knapweed spread into adjacent plant communities [44,509] (see <u>Succession</u>). Spotted knapweed seeds can also be transported in rivers and other watercourses [438].

## Seed Banking

Spotted knapweed has a persistent soil seed bank [105,455]; some seeds require seed aging, cool-moist stratification, freezing [126,169], or exposure to red light [342] to germinate (see Germination and Seedling Emergence). These requirements may enable some seeds to remain dormant in the soil seed bank for an extended period of time [105]. The proportion of seeds that enter the seed bank is small compared to yearly seed production and thus contributes relatively little to recruitment in established populations. The seed bank becomes more important to recruitment when the size of the seed bank equals or exceeds seed production, such as could occur during severe drought, after fire, or after mechanical or chemical removal of the adult population [455] (see Fire as a Control Agent and Control). The aerial seed bank is minimal because most spotted knapweed seeds are shed upon maturity and very few overwinter in seedheads [438,460].

Spotted knapweed seeds in the soil seed bank can be abundant, and mean densities as high as 60,690 seeds/m<sup>2</sup> have been reported. Viability of seeds in the soil seed bank is typically low (<14%), but varies among sites. Mean densities of viable seeds as high as 8,466 viable seeds/m<sup>2</sup> prior to seed dispersal have been reported [217,250,284,471,474] (table A5). Differences among sites in seed bank density and viability of seeds in the soil seed bank are due in part to site characteristics (abundance of spotted knapweed plants, presence of biological controls, and weather) and sampling methods (the timing of seed bank sampling and viability testing procedures). For example, at four sites in and near Missoula, Corvallis, and Hamilton, Montana, where spotted knapweed was dense (10–36 spotted knapweed stems/m<sup>2</sup>), seed bank density averaged 142 to 596 seeds/m<sup>2</sup> in 137-cm<sup>3</sup> soil cores in October, and at two sites near Corvallis and Stevensville, Montana, where spotted knapweed stems/m<sup>2</sup>) seed bank density averaged 142 to 596 spotted knapweed was "greatly reduced" by spotted knapweed biological control insects (0.3 spotted knapweed stems/m<sup>2</sup>) seed bank density averaged 24 and 47 seeds/m<sup>2</sup> in the same sample volume of soil [471]. In a spotted knapweed-invaded riparian meadow near Boulder, Colorado, where spotted knapweed cover averaged 32% of the total vegetation cover (ranging from 0% to 90% in plots), the density of seeds in 10-cm deep soil cores collected in October averaged 5,848 seeds/m<sup>2</sup> (ranging from 0 to 16,364 seeds/m<sup>2</sup>). However, 92% of

the seeds isolated from soils were shriveled, discolored, and/or partially decayed, and none of the tested seeds germinated after 14 days [250]. During 2 years at two sites near Bozeman, Montana, that varied in precipitation and aspect, seed production and viable seedbank density was higher at the site with higher available soil moisture [217].

Dormant, viable seeds can survive in the soil seed bank for at least 8 years [105]. Mean seed viability of buried spotted knapweed seeds in the field and laboratory-stored seeds is highest at dispersal and declines over time but can remain high for many years before declining [540]. Viability of exhumed spotted knapweed seeds buried in mesh packets declined over time and was higher, on average, in seeds buried 15-cm deep than seeds buried 2.5-cm deep at four dryland locations in Wyoming from 1 to 6 years after burial, although viability depended on location [540] (table 4). At two sites in Bozeman and Three Forks, Montana, <1% of spotted knapweed seeds buried 2.5-cm deep had germinated after 2.5 months, and 99% of ungerminated seeds were viable. After 12.5 months, 11% and 35% of buried seeds had germinated at each of the two sites, and viability of seeds that had not germinated was 91% and 96%, respectively [81]. At four sites in western Montana, spotted knapweed seed viability was about 10% after 2 years of burial at 5-cm deep [301]. At three sites in New York, survival of 1-year-old nongerminated seeds in field soils ranged from 0% to 9% after 3 years of burial [321]. Viability of laboratory-stored spotted knapweed seeds averaged 98% at the time of collection, 96% after 1 year of storage, 96% after 2 years, 91% after 4 years, and 64% after 7 years. In a greenhouse, viability of spotted knapweed seeds buried 1.3-cm deep in soil for 7 years averaged 29% [275].

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Depth of burial and	Site				Mean
time since buried	Laramie	Archer	Torrington	Sheridan	
2.5 cm					
1 year	37	7	6	7	14
2 years	28	9	5	6	12
4 years	19	2	1	2	6
6 years	3	0	0	2	1
15 cm					
1 year	55	39	22	22	35
2 years	42	19	27	18	27
4 years	34	11	7	7	15
6 years	10	6	2	1	5

Table 4—Viability (%) of exhumed spotted knapweed seeds buried in mesh packets at two soil depths 1, 2, 4, and 6 years after burial at four locations in Wyoming. Table modified from Wilson (2000) [540].

Control treatments conducted annually can reduce the number of spotted knapweed seeds in soil seed banks but it is likely to take several years to see effects [284,288]. Because of the importance of seeds in the soil seed bank to spotted knapweed reestablishment, researchers recommended use of one or more control treatments to deplete spotted knapweed seeds in the soil seed bank prior to revegetation efforts (e.g., [70,71,126,429]). If spotted knapweed is allowed to produce seeds after treatments, the seed bank can be quickly replenished [284,306].

Because seedhead-feeding biological control insect larvae can reduce <u>seed production</u> and viability they can also reduce seed bank densities [250,455,471], but declines may take years or even decades to manifest [471]. The average density of seeds in the soil seed bank at four sites 2 months after seed

dispersal in "robust" spotted knapweed populations was 281 seeds/m<sup>2</sup> compared with 19 seeds/m<sup>2</sup> at four sites where knapweed density had declined after being heavily infested with biological control insects for at least 30 years. Seed bank densities were much higher at two sites in central Montana (4,218 seeds/m<sup>2</sup>), where the insects have been established for a shorter period (10-15 years) [471]. For more information, see <u>Biological Control</u>.

#### **Germination and Seedling Emergence**

Spotted knapweed seeds may germinate shortly after maturity, and germination under laboratory and greenhouse conditions often exceeds 80% at maturity (e.g., [75,102,105,126,289,363,424,434,453,521]). However, many studies indicate a dormancy period for some portion of the annual seed crop. For example, Watson and Renney (1974) observed an increase in germination from 40% at maturity to 80% after 25 days of dry storage [524]. Under field conditions, studies reported that 35% to 89% of the seed crop was viable but did not germinate the year following dispersal [81,126,386]. This period of dormancy may be released by seed aging, cool-moist stratification, freezing [126,169], or exposure to red light [342]. On a single plant, spotted knapweed may have non-dormant seeds that germinate in the dark, light-sensitive dormant seeds that germinate after exposure to red light, and light-insensitive dormant seeds that germinate to red light. Variation in germination requirements enables seeds to germinate over time and facilitates the incorporation of seeds into the soil seed bank [342].

Only one study examined optimal soil moisture requirements for spotted knapweed emergence. A greenhouse study that examined soil moistures from 55% to 75% found that optimal spotted knapweed emergence occurred at 65% to 70% soil moisture content and seeds required more than 55% soil moisture to emerge from the soil [453].

Spotted knapweed seeds germinate over a range of temperatures. On a temperature gradient bar, spotted knapweed germinated over the entire temperature range studied from 7 to 34 °C and more than 80% germinated from 10 to 28 °C. Highest germination occurred at 19 °C [524]. In an incubator, highest germination percent and rate occurred from 15 to 25 °C in a study that examined temperatures from 5 to 30 °C. Dormancy may prevent germination at higher temperatures when soil moisture is fluctuating, and at lower temperatures when germination in late fall may make seedlings susceptible to winter kill. Germination after cold stratification provides a strategy for spring seedling emergence and avoidance of environmental extremes [126].

Spotted knapweed seeds germinate throughout the growing season whenever moisture and temperature are suitable. In some locations, such as in the Upper Midwest, seeds germinate throughout the growing season [101,543]. In other locations, such as in northwestern states and provinces, most seeds germinate in the spring, when soils are moist, but many also germinate in fall, particularly on sites that lack summer rain [217,462,524]. In western Montana, some seedlings emerge in fall, but most emerge in April and May, before most grasses break dormancy [81,126,302]. Because spotted knapweed seeds can germinate continuously throughout the growing season, spotted knapweed can occupy all of the available niches in a given habitat and outcompete neighboring plants [74]. In Montana, spotted knapweed "germinates abundantly in fall", when many native species are dormant and there are only low levels of native seed germination. This difference in "germination niche" appears to be an important contributor to spotted knapweed's invasiveness in the region [299,300,302].

Spotted knapweed seeds can germinate in light and dark and emergence decreases with planting depth [275,453,524]. In a greenhouse, optimal germination occurred in dark and alternating light and dark periods (87%) and optimal emergence occurred at the soil surface ( $\approx$ 90%) [524]. In another greenhouse study, 95% of seeds exposed to light at the soil surface germinated and emergence decreased with each increase in planting depth [275].

Spotted knapweed can emerge under open and closed canopies. In a greenhouse, spotted knapweed emerged equally well over a range of canopy cover, from 0% to 100% [453]. In experimental field studies in Montana, mean spotted knapweed plant biomass was 77% greater within "solid carpets" of native plants than in bare soil lacking native vegetation. The apparent facilitation of spotted knapweed by native plants may have occurred because it was easier for spotted knapweed seeds to germinate within existing vegetation compared to bare plots [300].

Other factors that affect spotted knapweed seedling emergence include <u>fire</u>, <u>soil biota</u>, and <u>biological</u> <u>controls</u>.

#### Seedling Establishment and Mortality

Seedling establishment is considered important in spotted knapweed population dynamics [289,441], although sensitivity analyses suggest that mortality at seed and seedling stages and the transition between them may have a low impact on population regulation [217].

Seedlings tend to have the highest mortality rates of all life stages [321]. Over 3 years on three sites in south-central and north-central New York, mortality of seedlings within their first year of growth (i.e., new seedlings) ranged from 45% to 93%. Overwinter mortality of established seedlings (i.e., seedlings entering their second year of growth as a rosette) ranged from 32% to 74%, while survival of flowering plants ranged from 35% to 78% [321]. A population model based on field observations in Bozeman, Montana, estimated the seedling mortality rate of spotted knapweed at 6.8% in spring and 72.5% in fall. The overwinter mortality rate was 48.3% for rosettes and 45.5% for flowering plants [217]. Other field studies reported mortality of seedlings from sown seeds ranging from 45% to <99% [289,524]. While in a common garden near Boulder, Colorado, seedling recruitment from sown spotted knapweed seeds (spotted knapweed plants present/spotted knapweed seeds sown) was low during 3 years (<1%); overwinter mortality rate was 40.6% from November of the first year to June of the following year [250].

Spotted knapweed seedling establishment, growth, and mortality depend primarily on environmental conditions at the time of establishment [530]. These include <u>weather</u>, <u>soil characteristics</u>, <u>plant</u> <u>competition</u>, <u>disturbance</u>, and spotted knapweed <u>propagule pressure</u>.

**Weather:** High spring precipitation appears to favor spotted knapweed seedling establishment [363], while below-average precipitation in spring [360] and summer [38] may lead to high seedling mortality [38] and reduced seedling density [360]. Spotted knapweed seedling establishment in undisturbed plots was positively correlated with April to June precipitation during 2 years ( $R^2 = 0.31$  and 0.36, n = 9) in steppe, shrub-steppe, and ponderosa pine sites in Washington, and about twice the number of seeded spotted knapweed, diffuse knapweed, and yellow starthistle seedlings established during a wet year than a dry year [363]. In a common garden in Missoula, Montana, spring spotted knapweed seedling density was lower in plots with below-average precipitation in spring (May and June) (50.0 seedlings/m<sup>2</sup>) than in plots with average precipitation in spring (73.3 seedlings/m<sup>2</sup>). Fall seedling densities were

similarly low between precipitation treatments (10.0 seedlings/m<sup>2</sup>) [<u>360</u>]. In a greenhouse study, experimental drought conditions resulted in increased mortality and decreased above- and below-ground biomass of spotted knapweed seedlings [<u>329</u>].

Limited data suggests that spotted knapweed seedling mortality may be high when conditions are dry following emergence [524]. At field sites in British Columbia, 12% of spotted knapweed seedlings died on average, but up to 55% died under dry conditions [438,524]. Seedlings may be particularly sensitive to drought because of an underdeveloped root system that is less effective at obtaining water than mature plants [289]. Adults may have enough root system for continued resource uptake and completion of their life cycle under dry conditions, but adult density appeared to be sensitive to low spring precipitation on a dry site near Bozeman, Montana [217].

**Soil Characteristics:** Soil characteristics that influence moisture, nutrient availability, and seed burial depth may also influence spotted knapweed seedling mortality, recruitment to the rosette stage, and growth. On three sites in south-central and north-central New York, causes of seedling mortality were unclear but included desiccation, likely enhanced by seedlings growing in well- to excessively-drained soils [321] (see <u>Soils</u>). Spotted knapweed recruitment may be high under low-nitrogen conditions. In a greenhouse, recruitment of spotted knapweed seedlings growing in monoculture and with slender wheatgrass for 80 days was higher for plants growing in low-nitrogen soils than in unamended control soils and high-nitrogen soils [250]. Spotted knapweed seedlings grow faster when they emerge from unburied seeds compared to buried seeds [83].

**Plant Competition:** Plant competition may reduce spotted knapweed seedling emergence and growth. In a greenhouse, competition with meadow fescue did not affect growth of spotted knapweed seedlings during early weeks, but strongly suppressed growth after 9 weeks [530]. In Corvallis, Montana, spotted knapweed seedling density was higher in low grass density plots (225 plants/0.25 m<sup>2</sup>) than in high grass density plots (112 plants/0.25 m<sup>2</sup>) [463]. Experimental clippings of Idaho fescue grown in pots with spotted knapweed resulted in increased seedling emergence and growth of spotted knapweed compared to unclipped controls. Soil water content increased with increased clipping levels and frequencies, resulting in a corresponding increases in spotted knapweed [216].

Spotted knapweed seedlings are more competitive for resources than associated vegetation when established before [425] or simultaneously with [71] associated vegetation. They are less competitive than associated vegetation when associated vegetation is dense and shades them [222]. Spotted knapweed establishment may be limited in native plant communities that have functional groups present that share close traits with spotted knapweed [386] (see <u>Revegetation</u>).

Competition with established plants may increase spotted knapweed seedling mortality, especially with reduced soil moisture availability. During experimental field studies at three sites near Boulder, Colorado, plant competition increased spotted knapweed seedling mortality at all sites except under increased water availability. During one study, emergence rates from sown spotted knapweed seeds ranged from 13.1% to 42.5%. Mortality of seedlings the following year ranged from 90.6% to 99.5% of sown seeds. Plots with intact vegetation trended towards higher mortality than plots with vegetation removed prior to seeding spotted knapweed. During a second study at one of the sites, below-average precipitation increased seedling mortality on all plots; however, even on watered plots, seedling

mortality was high. Of the 8,000 seeds sown in 40 plots in late March, by fall, only eight plants resulted, seven of which survived in watered plots with intact vegetation [289].

Spotted knapweed recruitment may be reduced on species-rich sites due to competition for resources such as water, but the relationship between spotted knapweed recruitment and species richness is inconsistent among studies, sites, and years [71,302]. For example, in a field experiment in southwestern Montana, seedlings of desirable species were planted in spring and spotted knapweed was sown in fall to simulate invasion of spotted knapweed into an established plant community. At one site, spotted knapweed recruitment was negatively related to desirable species richness ( $R^2 = 0.18$ , sample sizes not provided) 1 year after sowing, but 2 years after sowing, spotted knapweed recruitment was low, overall, and not related to species richness. At a drier site with shallow soil, spotted knapweed recruitment was not related to desirable species richness in either year. In another field experiment at the same locations, seeds of desirable species and spotted knapweed were sown simultaneously in spring to simulate revegetation of a site containing spotted knapweed seeds in the soil seed bank. One and 2 years after sowing, spotted knapweed recruitment was not related to desirable species richness at either site and 2 years after sowing, spotted knapweed dominated plots. Results suggested that establishing desired species early to maximize niche occupation with species that preempt soil water and controlling spotted knapweed recruitment from the soil seed bank may contribute to long-term revegetation success of spotted knapweed-invaded communities [71].

**Disturbance:** Disturbance creates favorable conditions for spotted knapweed seedling establishment by increasing bare ground, reducing litter and vegetation, and increasing sunlight to the soil surface [129,284,438,543]. Sites with intense disturbance (e.g., prolonged drought and overgrazing) that depletes multiple plant functional groups and reduces plant productivity are optimal for spotted knapweed establishment and spread [410] once moisture becomes suitable [289]. During 2 years, spotted knapweed seedling recruitment across nine sites in Washington was greater in plots where either biological soil crusts were removed or soil crusts and plants were removed than in undisturbed plots. Recruitment in undisturbed plots was very low (about 1%) [363]. On grassland sites with moderate to low densities of spotted knapweed in Montana, Switzerland, Romania, and Hungary, disturbance (all aboveground vegetation removed and the soil disturbed) and spotted knapweed propagule pressure increased spotted knapweed recruitment [301]. On the other hand, disturbances that bury plants may kill spotted knapweed. On three sites in south-central and north-central New York, burial of spotted knapweed plants due to erosion of sand dunes from heavy rains resulted in high mortality of all life stages [321].

Fire kills spotted knapweed seedlings [282,399], but mortality depends on the time of burning. Burning can create favorable sites for seedling establishment. For more information, see <u>Plant Response to Fire</u>.

Biological control insect larvae can increase mortality of spotted knapweed seedlings [<u>331</u>] and rosettes [<u>248,251,331</u>]. For more information, see <u>Biological Control</u>.

**Propagule Pressure:** Studies found that spotted knapweed is unlikely to establish unless large numbers of seeds are introduced at one time or small numbers of seeds are established on numerous occasions [30,407] (see Forests), and more seeds tend to produce more seedlings [30,407]. In a common garden near Boulder, Colorado, the total number of spotted knapweed seedlings present after 3 years was highest in plots sown with 2,000 seeds/m<sup>2</sup>/year than in plots sown with 1,000 or 500 seeds/m<sup>2</sup>/year

[250]. In a seed addition experiment in northwestern Montana, seedling survival increased with the number of seeds added during 2 years ( $R^2 = 0.27$  and 0.21, n = 100) with up to 2,500 seeds sown into 1.25-m<sup>2</sup> plots. Total survival was lower during a dry year than during an average precipitation year [455].

#### Plant Growth

Spotted knapweed grows quickly from the root crown in early spring [438,524] (see Seasonal Development). In Montana, spotted knapweed produces most of its growth from March to June [472]. Growth is slowed during the summer dry period in July. A second period of growth may occur if wet, cool weather follows the summer dry period [38]. Early spring growth gives spotted knapweed a competitive advantage over many natives for soil moisture and nutrients [269], and "the typical summer drought found in the semiarid steppe of Montana does not seem to pose a disadvantage to spotted knapweed" [94].

Many spotted knapweed plants live as rosettes for many years before bolting [38,101,472]. The time to bolting is influenced by the timing of germination and rosette size [332,424] (see Seasonal Development), weather, and competition for resources with other plants. At six spotted knapweed-invaded sites in Montana, the percentage of flowering plants during 1 year was low for 1- and 2-year-old plants and peaked in 5-year-old plants. During the following year, no 1- and 2-year-old plants flowered and the percentage of flowering plants peaked in 7-year-old plants. The later peak during the second year was attributed to drought [38]. In an old field in Corvallis, Montana, all bolted spotted knapweed plants were  $\geq 2$  years old. The percentage of bolted plants increased up to age 4 when 70% of plants bolted. Beyond age 4, the percentage of bolted plants increased only slightly. Delayed maturation of plants may have been due to plant competition or other stresses [472]. Another study found a large percentage of plants (up to 94%) bolted the year following sowing spotted knapweed seeds in a tilled field [424].

Spotted knapweed grows slower during dry than wet years [94,455,472] and dry than wet conditions [191]. In Corvallis, Montana, mean plant height was lower in a year with low March to June precipitation (44 cm tall, 99 mm precipitation) than a year with greater March to June precipitation (58 cm tall, 195 mm precipitation) [472]. In field plots in Corvallis, Montana, growth of spotted knapweed plants during a year with spring drought was lower than during a year of higher precipitation [94]. Spotted knapweed seeds collected from 13 populations in North America were grown in a greenhouse with water applied at two levels ("high stress" and "low stress"). The biomass of plants from 12 of 13 populations decreased from 5% to 50% (mean = 34% for all populations) in the high-stress treatment compared with the low-stress treatment, and only one population (Idaho) increased biomass slightly with water stress. Populations that produced large individuals also produced individuals that responded more negatively to water stress [191].

Spotted knapweed does not grow well in shaded sites [<u>111,243,318,319</u>] and spotted knapweed commonly grows in open areas [<u>5,10,101,243,295,415,524</u>] (see <u>Succession</u>). Root mass, foliage, and crown size are less in shade than full light [<u>243</u>].

Arbuscular mycorrhizal fungi may enhance spotted knapweed growth and contribute to its invasion success (e.g., [<u>180,296,396</u>]). For example, spotted knapweed produced greater total biomass when grown in soil inoculated with AMF spores collected from Custer County, Montana, than control soils [<u>396</u>]. Arbuscular mycorrhizal fungi increased spotted knapweed growth in a riparian chronosequence

along a floodplain in Flathead County, Montana. In soils collected across the chronosequence, spotted knapweed grew larger with AMF in 7 of 8 soils tested than without AMF, demonstrating that it responds to AMF across a wide range of soils that differ in physical and chemical properties and AMF inoculum potential [180]. However, some studies found that spotted knapweed plants grown with AMF were always smaller than plants grown without AMF [422,478] (see Soil Biota).

**Plant Competition:** Competition for resources (e.g., light, water, and nutrients) with associated vegetation can reduce density (mature plants and rosettes) [224,386,463], shoot length and height [332], shoot number [332], shoot and root biomass [332,386,457], shoot:root ratio [457], and survival [332] and increase the time to bolting [457] of spotted knapweed plants. Multiple stress factors (e.g., increased plant competition, herbivory by biological controls, drought, and/or low nitrogen) can have additive negative effects on spotted knapweed growth and survival [335,376]. Disturbances that reduce competition and increase space and soil nutrient availability result in increased spotted knapweed growth [149]. Spotted knapweed can also reduce the biomass of associated vegetation by reducing soil nitrogen, water, and light available to them [145,187,206,300]. For example, bluebunch wheatgrass growth, reproduction, and recruitment are lower when grown with spotted knapweed than when grown alone [360].

Intraspecific competition may be more important than interspecific competition in some cases [218,293]. High conspecific density may reduce shoot length, shoot weight [218,332], shoot number [332], shoot:root ratio [335], biomass [293,332], and survival [332], and increase cover [389] and height [389] of spotted knapweed plants. For example, at two sites in western Montana, spotted knapweed biomass per plant in common gardens was negatively correlated with spotted knapweed density ( $R^2 = 0.17$ , n = 192;  $R^2 = 0.24$ , n = 128) [293]. Spotted knapweed plants were larger and produced more stems and viable seeds when adjacent to bluebunch wheatgrass plants compared to conspecifics, suggesting that spotted knapweed plants faced weaker interspecific than intraspecific competition [360]. Spotted knapweed roots exude (±)-catechin that may act as an autoinhibitory as well as an allelochemical [379,381] (see Allelopathy).

Some studies reported that spotted knapweed is more efficient at acquiring soil nitrogen [36,149,347] and soil phosphorus [187,495] than some of its native competitors, and spotted knapweed invasion success has been attributed to its ability to outcompete native species for soil nutrients [187,270,349,495], while other studies reported that some native species may be better at acquiring soil nutrients than spotted knapweed (e.g., [36,250,347]). Spotted knapweed biomass may be greater in high-nitrogen than low-nitrogen soil (e.g., [248,250,293,435]), but effects of added nitrogen depend on the presence of plant competition [250]. For example, total spotted knapweed seedling biomass was 62% and 149% higher, respectively, in greenhouse plots with high amounts of added nitrogen than in unamended control plots and plots with low amounts of nitrogen. When grown with native slender wheatgrass, spotted knapweed biomass was reduced to near zero in plots with high amounts of added nitrogen, indicating that spotted knapweed was not able to take advantage of the high amounts of added nitrogen in the presence of slender wheatgrass, and slender wheatgrass was able to outcompete spotted knapweed. Low soil nitrogen conditions improved spotted knapweed recruitment into plots with slender wheatgrass, although biomass was still below the levels reached in the absence of competition, suggesting that low nitrogen conditions could increase the invasion success of spotted knapweed [250].

Earlier and deeper root development of spotted knapweed than bluebunch wheatgrass suggests that bluebunch wheatgrass may be a poor competitor with spotted knapweed. In southwestern Montana, spotted knapweed roots developed earlier and with a higher proportion of deep roots than bluebunch wheatgrass; 39% of spotted knapweed roots and 25% of bluebunch wheatgrass roots were deeper than 30 cm. In addition, AMF colonization of spotted knapweed was higher than that of bluebunch wheatgrass [296]. On the other hand, spotted knapweed grows slower than that of nonnative intermediate wheatgrass and crested wheatgrass. For example, after 70 days of growing in pots, spotted knapweed mean total dry weight/plant, dry root weight/plant, and mean maximum rooting depths were lower than those of intermediate wheatgrass may be good candidates for revegetation of sites previously dominated by spotted knapweed because of their potential to preempt resources [71] (see <u>Revegetation</u>).

## Plant Mortality

Spotted knapweed plants can live to 12 years or older [<u>38</u>] (see <u>Plant Longevity</u>), and mortality rates vary with age [<u>472</u>]. In Corvallis, Montana, spotted knapweed mortality was estimated in spring and fall during 2 consecutive years. Mortality was 44% from age 3 to age 4, 31% to age 5, 20% to age 6, and 38% to age 7 [<u>472</u>]. Severe winter weather may "occasionally" kill spotted knapweed plants [<u>524</u>].

Spotted knapweed mortality may increase during drought [321,360], and young plants may be more susceptible to drought-caused mortality than older plants [38,455]. In New York, survival to flowering of spotted knapweed plants was lower during a drought year (35%) than during 2 wetter years (60%–78%) [321]. At six sites in western Montana during an average precipitation year (1984), most spotted knapweed plants were in the youngest age classes (2-3 years old) with fewer plants in the oldest age classes (up to 12 years old). During the following summer drought (1985), most plants were in the older age classes. The authors stated that "These changes were undoubtedly due to higher mortality among the younger age classes than among the older age classes during the 1985 drought" [38]. On spotted knapweed-invaded sites in northwestern Montana, mortality of adult spotted knapweed plants was low during 2 years even though these years were dry and one was "extremely so". The researcher suggested that because the previous 4 years were normal to wet, and the plants were well-enough established, the plants could withstand a couple of dry summers. However, spotted knapweed seedlings that survived the drought took "a very long time to become adults", and most did not become adults in the 2.5 years of the study [455]. Although spotted knapweed mortality may increase during drought, disturbances such as drought can deplete native species abundance and create conditions for subsequent spotted knapweed invasion [410] (see <u>Maintaining Desirable Vegetation</u>).

In addition to reducing seed production, biological control insects can reduce rosette [93,94,288,289,333] and adult (flowering plant) [288,360] survival as well as reduce spotted knapweed height and biomass (e.g., [93,94,248]), but the effect of biological controls on spotted knapweed mortality and growth, and ultimately population density and dominance, are complex in part due to spotted knapweed's ability to compensate for mortality and loss of biomass due to herbivory (e.g., [60,248,332,360,365,376,404,457]).

## Vegetative Reproduction and Regeneration

Spotted knapweed can reproduce vegetatively from lateral roots just below the soil surface that form new rosettes adjacent to the parent plant. Multiple rosettes stemming from a single spotted knapweed

root crown are common [<u>101,438,524</u>]. In a greenhouse study, spotted knapweed produced 5.8 new rosettes/plant after flowering and senescing [<u>50</u>]

Spotted knapweed often sprouts and forms new shoots and flowers after being defoliated or top-killed (e.g., [28,129,139,324,417,469,491]) (see Seed Production and Predation). Sprouting and subsequent flowering success depends on defoliation timing, weather, and frequency. Surviving plants may sprout and flower after low-severity fire that does not damage the root crown if the fire occurs before plants have bolted. In Augusta, Michigan, surviving spotted knapweed plants produced flowering stems after a low-severity spring prescribed fire that occurred before plants had bolted. However, surviving plants did not produce flowering stems after a low-severity summer prescribed fire that occurred when spotted knapweed plants were starting to flower [129] (see Immediate Fire Effects). In Washington County, Arkansas, mowed spotted knapweed plants sprouted and produced seeds the same growing season if mowed to 10 to 13 cm tall in May (before flowering), June (start of flowering), and July (peak flowering and beginning of seed set) but not in August (seed set). Drought conditions during 1 year of the study, led to failure of mowed plants to sprout that growing season regardless of the timing of mowing [324]. In Missoula, Montana, Aschehoug (2011) also noted a lack of sprouting in spotted knapweed during drought [14]. In a greenhouse, spotted knapweed sprouting success decreased with increased clipping frequency from once to twice at 2 cm above the root crown. Individual spotted knapweed plants from 13 locations in North America that were flowering prior to clipping had a higher sprouting success than those that were not flowering [417].

#### SUCCESSIONAL STATUS

#### Shade Tolerance

Spotted knapweed seeds can <u>germinate</u> under a closed canopy [453], but mature plants are uncommon in shaded areas [<u>111,524</u>]. Spotted knapweed plants are typically found under open canopies [<u>5,10,101,243,295,415,524</u>]. In Yellowstone National Park, spotted knapweed was always found in areas with <20% canopy cover, and 75% of its occurrences had ≤5% canopy cover. On Long Island and in the Adirondacks, New York, open, disturbed areas with low tree cover were associated with greater distribution of spotted knapweed, suggesting that forested, shaded areas in these regions are less susceptible to spotted knapweed invasion as long as they remain relatively free from disturbance, but meadows, grasslands and disturbed, open areas are likely to be highly susceptible to invasion [<u>5</u>]. In western Montana, spotted knapweed is much less abundant under ponderosa pine canopies than in surrounding open grassland [<u>318,319</u>].

#### **Succession**

Spotted knapweed frequently occurs in early-successional forests (e.g., [143,167]), but is uncommon in older stands (e.g., [167]). In grand fir/bride's bonnet habitat type in the Selway-Bitterroot Wilderness, Idaho, spotted knapweed was a dominant understory forb in a burned 15-year-old stand but not found in a nearby burned 215-year-old stand [167]. Spotted knapweed is common in old fields [73,77,101,144,518,551] and has been reported in mid-successional grasslands [164]. Hironaka (1990) presents a replacement series of weedy species in Intermountain rangelands in which summer annuals are replaced by winter annuals (e.g., Russian-thistle is replaced by cheatgrass), and the earlier winter annuals are replaced by later maturing annuals and perennials (e.g., cheatgrass is replaced by medusahead or knapweeds) [205].



Figure 4—Spotted knapweed plants growing along a roadside. Photo by Steve Dewey, Utah State University, and courtesy of Bugwood.org.

Disturbance creates favorable conditions for spotted knapweed seedlings [129,284,438,543] (see Seedling Establishment and Mortality) and spotted knapweed is common on disturbed sites (e.g., [5,16,95,176,295,412,426,509,519,524]). In the Northeast, spotted knapweed occurs "almost exclusively" in open, disturbed sites [5]. In southern interior British Columbia, spotted knapweed density was positively correlated with the degree of soil disturbance [524]. In western Montana, spotted knapweed invasion success increased with site disturbance and soil moisture stress (see Soils). Disturbance severity had the greatest influence in moist forest habitat types. In grass and shrub habitat types, southern aspect and disturbance severity contributed to spotted knapweed invasion success [326]. Spotted knapweed also commonly occurs in burned areas (e.g., [137,138,160,385,502]) (see Plant Response to Fire), on firelines [16] (see Fire as a Control Agent), and in riparian habitats with sand or gravel bars disturbed by annual flooding and ice jams [176] (see Plant Communities).

Spotted knapweed usually establishes shortly after disturbances that open up the tree canopy. In western Montana, for example, spotted knapweed invades when the dominant species from ponderosa pine/redosier dogwood or black cottonwood/redosier dogwood riparian site types have been removed [<u>179</u>]. In addition, spotted knapweed is common in burned [<u>137,138,160,385,502</u>] (see <u>Plant Response</u>

to Fire) and logged [<u>11,142,343,415</u>] forests. In Washington, a total of 10,368 ha (25,620 acres) of spotted knapweed was reported from 19 counties by Roche in 1990. Ninety-two percent of the total area occurred on disturbed forest and timbered range sites [<u>415</u>].

However, spotted knapweed does not always require disturbance to establish. It invades relatively undisturbed native perennial plant communities in the northern Intermountain region and adjacent open, ponderosa pine woodlands [110,138,152,260,437,508,509], and it invades wilderness areas in Montana [257]. In Glacier National Park, spotted knapweed established in rough fescue grasslands adjacent to roadside spotted knapweed populations presumably due to abundant seed sources on roadsides [508]. The numerous breaks in cover, which provide favorable light conditions for seed germination, and the warm-dry climate of these grassland ecosystems appears to facilitate invasion of spotted knapweed and other nonnative species [342,508]. Spotted knapweed invades "large expanses of rangeland" [262] including rangelands in "high ecological condition" [552] and those with "high levels of livestock disturbance" [152].

In its native range, spotted knapweed occurs more frequently in "man-made" habitats such as transportation corridors and quarries than in natural or semi-natural habitats [362]. Spotted knapweed is associated with similar habitats in its invaded North American range and it frequently establishes along transportation corridors (e.g., [7,30,99,101,152,366,508,524]), where it can then spread into adjacent disturbed and undisturbed communities [44,326,508] (see <u>Site Characteristics</u>). In riparian areas in the Interior Columbia River and Upper Missouri River basins, occupancy models indicated that spotted knapweed was positively associated with road density and ambient temperature and negatively associated with percent of riparian area grazed [7].

Spotted knapweed establishment on sand dunes may contribute to their stabilization. In Michigan, along Lake Superior, spotted knapweed invasion contributed to the stabilization of sand dunes at a more rapid rate than would occur through natural succession and areas with spotted knapweed had reduced cover of bare sand [305].

## FIRE ECOLOGY AND MANAGEMENT

## **IMMEDIATE FIRE EFFECTS**

Severe fire can kill spotted knapweed plants, but low-severity fire that does not damage the root crown is unlikely to kill them [111]. Winston et al. (2012) commented that the stout taproot of *Centaurea* spp. is likely to survive most fires [543], and Czarapata (2005) stated that burns that remove nearly all the duff are most effective at killing spotted knapweed roots, but "normally succeed only in newly infested areas" [101].

Spotted knapweed sprouts after fire [129,310]. If low-severity fire occurs prior to bolting, spotted knapweed plants are likely to sprout and produce flowering stems in the same growing season [129]. McGowan-Stinski (2001) observed spotted knapweed plants sprouting three to four times following repeated spot burning during the growing season [310]. Reports of spotted knapweed sprouting after other methods of defoliation are common (e.g., [28,139,324,417,469,491]) (see Vegetative Reproduction and Regeneration).

Heating or burning of seeds generally reduces spotted knapweed germination and seedling emergence [3,131,282,517]. Spotted knapweed seeds heated in a furnace at 200 °C for 120 seconds or more and seeds heated at 400 °C for 30 seconds or more had lower germination (0.6%–4.5% and 0.6%–6.1%, respectively) than unheated control seeds (50%) [3]. Spotted knapweed seed germination was similarly low (9.5%–11.3%) following low- and high-intensity fires in pots [282], but higher than that reported for heated seeds by Abella and MacDonald (2001) [3]. The researchers suggested that the experimental fires in their study were likely of lower intensity or of shorter duration than those in Abella and MacDonald's (2000) [3] study, and "may not have fully simulated the effects of a burn in a grassland" [282]. Following a single experimental fire in a laboratory, about 15% of seeds germinated after they were burned with the lowest fuel load  $(100 \text{ g/m}^2)$  compared with 97% for unburned seeds. Germination rates declined with increasing fuel load, and no spotted knapweed seeds germinated after they were burned with the highest fuel load (700 g/m<sup>2</sup>) [517]. Near Augusta, Michigan, spring prescribed fire reduced spotted knapweed seedling emergence in fall by 50% relative to an unburned control, while summer prescribed fire reduced spotted knapweed seedling emergence in fall by 66% [131]. While germination and seedling emergence may be reduced by fire, fire may enhance sites for seedling establishment [129], and even a small percentage of seeds surviving to establish can be sufficient to reestablish a site [424] (see Seed Production and Predation).

Spotted knapweed survival following fire depends on the life stage and time of burning, with seedlings tending to be most sensitive to fire during spring. Adult plants are less sensitive to season of fire [131,282]. In tallgrass prairie remnants Near Augusta, Michigan, the density of seedlings surviving in plots burned under prescription in spring and summer was less than that on unburned plots, but density in plots burned in fall was similar to that in unburned plots. The density of juveniles was less on plots burned in summer than on unburned plots, but density in plots burned in spring and fall was similar to unburned plots. The density of juveniles was less on plots season burned plots. The density of adults was similar among burned and unburned plots, regardless of season burned [131]. In a greenhouse study, seedlings in the cotyledon stage and seedlings with one or two primary leaves were killed by low- and high-severity fire. Because seedlings were "very sensitive" to fire-caused mortality, spring prescribed fires that kill spotted knapweed seedlings are likely to be effective in reducing spotted knapweed establishment, but the authors cautioned that their results "do not suggest that fire would kill the older, deeply-rooted rosettes" [282] (see Fire as a Control Agent).

#### **POSTFIRE REGENERATION STRATEGY**

Herbaceous root crown, growing points in soil Ground residual colonizer (on site, initial community) Secondary colonizer (on- or off-site seed sources) [459]

#### FIRE ADAPTATIONS

Spotted knapweed is a perennial or biennial (sometimes annual) forb that produces abundant seeds (see <u>Seed Production and Predation</u>). It can establish after fire either from undamaged seeds in the soil seed bank (see <u>Postfire Seed Banking</u>), from seeds dispersed from off-site sources, or from sprouting plants that survive the fire. While germination and seedling emergence are likely to be reduced by fire [3,282,517] (see <u>Immediate Fire Effects</u>), fire is likely to create conditions that are favorable for spotted knapweed seedling establishment by increasing bare ground, reducing litter and vegetation, and increasing sunlight at the soil surface [129,284,438,543] (see <u>Postfire Seedling Establishment</u>). Spotted knapweed has a large, perennial taproot and is likely to survive and sprout after fire if the root crown is not killed [310].

#### PLANT RESPONSE TO FIRE

Most information about spotted knapweed's response to fire comes from field studies using prescribed and experimental fires—alone and in combination with other methods—to control invasive populations of spotted knapweed. Some studies examined spotted knapweed abundance after wildfires. Information regarding spotted knapweed's response to fire alone is summarized below. For a summary of its response to fire in combination with other control methods, see <u>Integrated Management with Fire</u>. Most studies about spotted knapweed's response to fire were conducted in <u>forests</u>, <u>tallgrass prairies</u>, <u>and other warm-season grasslands</u>. A few studies were conducted in <u>bunchgrass steppes</u>. Studies primarily examined changes in spotted knapweed abundance and population growth after fires, but studies from tallgrass prairies and other warm-season grasslands also included information about postfire reproduction, seed banking, and seedling establishment. Information on germination, seedling emergence, and seedling establishment also comes from common garden, greenhouse, and laboratory studies. Spotted knapweed abundance may increase, decrease, or be unaffected by fire in the short term. Its response to fire varies among sites, plant communities, and fire characteristics (season, frequency, intensity, and severity). Table A6 provides information on studies about spotted knapweed's response to fire.

## **Forests**

## **Postfire Abundance**

After fire in forests, spotted knapweed abundance may increase or decrease depending on forest habitat type [137], time since fire [137], fire intensity and severity, fire season [11,137,343], and propagule pressure from spotted knapweed [30].

Abundance Following Wildfires: Information on spotted knapweed's response to wildfires in forests is limited. In Montana, spotted knapweed commonly occurs in forests burned by wildfire [137,138,160,320,385,502], and tends to increase in cover with time-since-fire. Within 2 weeks of fire, spotted knapweed cover can exceed that of other vegetation [160]. Spotted knapweed cover in a ponderosa pine/chokecherry habitat type after a severe August wildfire in Lame Deer, Montana, was about 17% and 37% in postfire years 1 and 2, respectively. No information on prefire spotted knapweed cover was given [385]. In Douglas-fir forest in western Montana, spotted knapweed was not recorded 3 years after a "severe stand-destroying" wildfire but was reported 5 to 10 years after the fire [502]. In burned areas on four national forests in western Montana, spotted knapweed occurred most frequently in Douglas-fir and ponderosa pine habitat types and least frequently in subalpine fir habitat types. Its occurrence was highest in burned areas of lower burn severities in the first few years after fire, but its occurrence increased over time in burned areas of higher burn severities. Occurrence in unburned areas was not provided. Of the four national forests studied, it was most abundant on the Bitterroot National Forest, where its cover increased from 19.4% in plots 1 or 2 years after fire, to 26.1% 3 years after fire, 37.1% 5 years after fire, and 41.3% 7 years after fire [137,138].

<u>Abundance Following Prescribed Fires:</u> Spotted knapweed abundance in Douglas-fir and ponderosa pine communities in western Montana may increase after prescribed fire [<u>11</u>,<u>343</u>], and may increase more after low- than high-severity spring prescribed fire [<u>11</u>], although one study reported no spotted knapweed after fire despite nearby seed sources [<u>204</u>]. In western Montana, in a Douglas-fir/mallow ninebark habitat type, spotted knapweed was present before a fall prescribed fire, but absent in postfire year 1. In postfire year 2, spotted knapweed volume was double the preburn volume [<u>343</u>]. Spotted

knapweed cover increased after both high and low fuel consumption spring prescribed fires (40% and 20% duff reduction, respectively) following shelterwood cuts in Douglas-fir-ponderosa pine communities in western Montana. Spotted knapweed cover was highest on high-consumption fire sites, both before and after treatment, but its relative increase was greatest on low-consumption fire sites across all four postfire years [11] (table 5). Twenty-tree years after both cutting and burning treatments, spotted knapweed cover averaged 1% [226]. In ponderosa pine and Douglas-fir forests near Kamloops, British Columbia, spotted knapweed was not detected in May, June, or July in either of two sites 1 and 2 years after low-severity March prescribed fires. Prefire data were lacking, but spotted knapweed abundance on portions of the sites and in nearby areas was low to moderate [204].

Table 5—Changes in spotted knapweed cover during the 4 years following shelterwood cutting and prescribed fire in Douglas-fir-ponderosa pine communities in Lick Creek, Montana. Modified from Arno (1999) [11].

Treatment	Average percentage spotted knapweed cover					
		(% change relative to before fire)				
	Before	Postfire	Postfire	Postfire	Postfire	
	fire	year 1	year 2	year 3	year 4	
Unburned	0.3	0.4 (33.3)	0.6 (100.0)	1.4 (366.7)	1.9 (533.3)	
control						
Low-	0.5	1.0 (100.0)	3.4 (580.0)	4.9 (880.0)	5.9 (1,080.0)	
consumption fire						
High-	1.9	3.6 (89.5)	7.3 (284.2)	11.4 (500.0)	14.1 (642.1)	
consumption fire						

In lodgepole pine forest at the Tenderfoot Creek Experimental Forest, Montana, spotted knapweed occurred with very low abundance along newly constructed forest roads, but it did not spread into nearby burned or thinned treatment units during the first 9 posttreatment years. The lack of spread may have been due to the overall low abundance of spotted knapweed in the study area [30]. Other studies reported spotted knapweed spreading from roads into adjacent disturbed and undisturbed communities [44,326,508] (see Succession).

## **Growth in Burned Soils**

In a greenhouse using burned soils collected from mixed-conifer forest on the eastern slope of the Cascade Range, Oregon, spotted knapweed had 85% less biomass when grown in red soil (severely burned soil) than black soil (less severely burned soil). Soil nutrients, percent colonization of spotted knapweed by AMF, and soil microbial abundance were all lower in red than black soils [192,193].

## Bunchgrass Steppe

## **Postfire Abundance**

Few studies examined spotted knapweed's response to fire in bunchgrass steppe and available information is conflicting. In perennial bunchgrass steppe in Missoula, Montana, cover of nonnative perennial forbs, primarily spotted knapweed and Dalmatian toadflax, on burned areas 1 year after a July wildfire (≈18%) was less than that on unburned areas (≈25%), but statistical differences were not determined [29]. For more information on this study see Fire as a Control Agent. On a northeastern Washington rangeland, Sheley and Roche (1982) conducted a study on the effects of prescribed fire and

other control methods on spotted knapweed, but gave no information on the characteristics of the fire or comparisons to controls [430]. However, Sheley et al. (1999) interpret this study as suggesting that "a single, low-intensity fire increased the cover and density of this weed without improving the residual, desirable understory species" [438]. For more information on this study, see Integrated Management with Fire.



Figure 5—A firefighter uses a drip torch to ignite a 5-ha burn unit in a steppe community at the Big Hole National Battlefield's Howitzer Hill, Montana, in September 2014. The objectives of the burn were to promote long-term persistence of Lemhi penstemon (a rare plant), reduce encroachment by lodgepole pine, and slow the spread of spotted knapweed. Photo courtesy of the National Park Service.

In a common garden study in Missoula, Montana, spotted knapweed cover was higher on droughtburned plots than on undisturbed plots within experimental bunchgrass assemblages. Spotted knapweed was seeded onto plots with various transplanted native bunchgrass seedling assemblages representing low, medium, and high native species richness. Spotted knapweed cover on plots with experimentally reduced rainfall followed by a low-intensity August experimental fire (drought-burned plots) was higher (about 64%, 46%, and 28% at low, medium, and high species richness, respectively) than on undisturbed control plots with ambient rainfall (about 58%, 20%, and 6%, respectively), regardless of species richness level [382].

## Tallgrass Prairies and Warm-season Grasslands

#### **Postfire Abundance and Population Growth**

Many published studies in Michigan examined spotted knapweed abundance after fire in tallgrass prairies and other warm-season grasslands and most of these studies found reduced spotted knapweed abundance following frequent fire [129,131,201,280,285,384], but results depended on prefire spotted knapweed abundance and phenology, fire intensity and severity, weather, and fire season [129,131,282,285,384]. Spring burns can be effective at reducing spotted knapweed abundance if they are of high enough intensity and severity, but summer burns may be most effective [129,131,282,285,384]. Spotted knapweed abundance is likely to increase after cessation of frequent burning if on- or off-site seed sources are available [283].

In Augusta, low-severity annual summer prescribed fires reduced the total numbers of spotted knapweed plants four to eight times compared with unburned controls, while total numbers following low-severity alternate-year summer prescribed fires and low-severity annual and alternate-year prescribed fires in spring and fall were not different from controls in any year (table 6). Among annual and alternate-year prescribed fires in spring, summer, and fall, annual summer prescribed fires were the only treatment that resulted in spotted knapweed population decline (growth rate = 0.59), while populations grew in control plots (growth rate = 1.17). Summer prescribed fires occurred when spotted knapweed plants were starting to flower, and consecutive summer prescribed fires reduced population growth by reducing reproduction. Populations burned only in alternate years showed no significant reduction in population growth rates, probably because of the high reproductive output of spotted knapweed plants in the off-burn year (2002; table 6) [129] (Postfire Reproduction).

Table 6—Average number of juveniles, nonreproductive adults, small adults, large adults, and seeds per 0.25 m<sup>2</sup> for each treatment during 3 years in Augusta, Michigan.

Treatments included annual prescribed fires in 2000, 2001, 2002, and 2003 and alternate-year spring prescribed fires in 2001 and 2003. Juveniles were first-year plants, small adults had one stem, and large adults were multistemmed. Asterisks indicate significant differences from control values: \*\*P  $\leq$  0.01, \* P  $\leq$  0.05,  $\frac{1}{7}$  P < 0.10. Data with asterisks are bolded. Table reproduced from Emery and Gross (2005) [129].

Year and	Number	Number of	Number	Number	Total	Seed
treatment	of	nonreproducing	of small	of large	number of	production
	juveniles	adults	adults	adults	plants	
2001	1		1			1
Control	11.13	1.38	2.25	1.63	16.4	147.5
Annual	6.75	2.00	1.00	1.50	11.3	83.5
spring				-		
Alternate	17.25	0.75	1.50	1.50	21.0	60.1*
spring				-		
Annual	2.50	0.00	1.00	1.25	4.8*	1.2**
summer						
Alternate	5.25	0.50	2.25	2.50	10.5	0.0**
summer						
Annual fall	7.50	0.25	1.00	0.50	9.3	192.8
Alternate fall	10.75	0.25	3.50	1.00 <del> </del>	15.5	311.8
2002			1		1	1
Control	11.00	8.00	4.50	2.38	25.9	512.8
Annual	10.00	6.50	2.25	1.50	20.3	439.8
spring						
Alternate	5.25	9.50	6.25	2.25	23.3	535.8
spring						
Annual	0.25**	2.50	1.00*	1.00	4.8*	19.3*
summer						
Alternate	2.75 <del> </del>	3.75	3.00	3.25	12.8 <del> </del>	644.3
summer						
Annual fall	7.75	5.25	1.25*	1.00	15.3	295.8
Alternate fall	12.00	7.00	3.75	3.25	26.0	800.3
2003						
Control	5.33	12.67	4.00	2.67	24.7	346.0
Annual	2.00	14.33	2.00	1.00	19.3	211.5
spring						
Alternate	2.67	10.00	3.33	3.33	19.3	369.1
spring						
Annual	0.00**	0.67**	1.67	0.67	3.0**	201.9
summer						
Alternate	1.67	4.33 <del> </del>	1.67	3.67	11.3	83.3
summer						
Annual fall	2.00 <del> </del>	9.00	0.33 <del> </del>	1.33	12.7	70.5
Alternate fall	2.33	6.00	5.67	3.33	17.3	413.3

In reconstructed mesic tallgrass prairie in Barry County, repeat experimental fires reduced median spotted knapweed cover and biomass in the short-term regardless of burn season (spring or summer) and temperature (low or high intensity), although summer fires were more effective than spring fires at reducing spotted knapweed cover and biomass, overall (table 7). The August following the second fires, unburned (but clipped) control plots tended to have higher spotted knapweed cover and biomass than burned plots. Spotted knapweed cover was lower in summer-burned plots than in spring-burned plots, with the lowest cover found in plots burned at low and high intensity in summer and the highest cover found in control plots and plots burned at low intensity in spring. Burning at both temperatures and seasons resulted in lower spotted knapweed biomass in burned than control plots, with the lowest biomass found on plots burned at low and high intensity in summer [<u>384</u>].

Table 7—Approximate median spotted knapweed cover and biomass at the end of the growing season in August following two consecutive low- or high-intensity spring or summer prescribed fires in reconstructed tallgrass prairie in Barry County, Michigan.

Low-intensity burned plots were burned with a propane torch to reach 103 °C and high-intensity burned plots were burned to reach 316 °C in mid-May (spring) and late June (summer). Control plots were clipped with a weed trimmer in spring or summer of the first year. Median values within each variable that do not differ share a letter are significantly different ( $P \le 0.05$ ). Data estimated from Figure 1 in Pitman and Aschenbach (2019) [384].

Spring	Summer			
45a	23ab			
22ab	2cd			
15bc	3d			
Biomass (g/0.1 m <sup>2</sup> )				
4a	3ab			
1bc	1c			
1bc	0.5c			
	45a 22ab 15bc 4a 1bc			

In restored warm-season grasslands at the Bass River Recreation Area, Michigan, density of spotted knapweed seedlings, juveniles, and adults was generally lower on burned than unburned plots following annual mid-spring prescribed fires during a 3 year study (<u>table 8</u>). Spotted knapweed biomass and dominance were lower in burned than unburned plots each year and declined in both burned and unburned areas [<u>285</u>]. However by 8 years after the last fire, spotted knapweed total biomass and dominance were similar between burned and unburned plots [<u>283</u>].

Table 8—Fire effects on spotted knapweed biomass and dominance in restored\* tallgrass prairies at the Bass River Recreation Area, Michigan, in August, following mid-spring (late April to late May) prescribed fires in 2003, 2004, and 2005.

Means for a single variable and year followed by different letters are statistically different at P < 0.05. Data from 2003, 2004, and 2005 are from MacDonald et al. (2007) [285]. Data from 2013 are from MacDonald et al. (2014) [283].

Variable and	Year				
treatment	2003	2004	2005	2013	
Seedling density (	plants/m <sup>2</sup> )				
Unburned	≈5a	≈75a	≈2	No data	
Burned	≈1b	≈28b	≈1	No data	
Juvenile density (	plants/m <sup>2</sup> )				
Unburned	≈2.2	≈4.0a	≈3.2a	No data	
Burned	≈0.4	≈2.8b	≈1.1b	No data	
Adult density (pla	nts/m²)				
Unburned	≈3.0a	≈1.7a	≈1.2a	No data	
Burned	≈0.3b	≈0.2b	≈0.4b	No data	
Biomass (g/m <sup>2</sup> )	Biomass (g/m <sup>2</sup> )				
Unburned	74.4a	30.9a	5.2a	1.9	
Burned	7.2b	5.7b	0.9b	2.3	
Dominance (% of	Dominance (% of total biomass)				
Unburned	12.1x	5.7x	2.1	1.1	
Burned	2.5y	1.6y	0.5	1.5	

\*Plots were treated with herbicides, tilled, fertilized, and seeded with warm-season grasses in various combinations in 1999 as described in MacDonald et al. (2003) [281].

In an adjacent study area at the Bass River Recreation Area, burning treatments had little effect on spotted knapweed density and biomass. Juvenile and adult density and total biomass were similar in mid-July between restored plots burned at low severity in early April 2012 (a drought year) and unburned, restored plots, but seedling density was higher on burned plots [284,306]. Plots were burned again in 2014, 2015, and 2016 at relatively higher severity (table 9). In 2015 and 2016, spotted knapweed seedling, juvenile, and adult densities in restored, burned plots were similar to those in restored, untreated plots, except juvenile density was lower in burned than untreated restored plots in 2015. In addition, relative cover of spotted knapweed was similar between burned and unburned plots from 2013 to 2016 [280]. See <u>Postfire Seedling Establishment</u> for more information on this study.

Differences among the aforementioned studies in the effects of spring burning soon after single or consecutive annual prescribed fire were probably due to differences in grassy fuel loads and/or weather that affected fire intensities and severities. Study areas with lower spotted knapweed abundance, higher fuels loads, and weather conditions that resulted in higher intensity and severity fires in spring (i.e., [280,285]) had greater reductions in spotted knapweed abundance than study areas with higher spotted knapweed abundance, lower fuel loads, and weather conditions that resulted in lower intensity and severity fires in spring (i.e., [129,280,284]). Pitman et al. (2019) concluded that while spring burns in tallgrass prairies can be effective at reducing spotted knapweed abundance, even when of low intensity,

summer burns are likely most effective because reducing spotted knapweed abundance during the flowering stage in summer reduces seed production and viability as well as abundance [384].

Table 9—Mean spotted knapweed density (number/m<sup>2</sup> (SE)) in 2015 and 2016 following prescribed fire in April of 2012\* and May of 2014, 2015, and 2016\*\* at the Bass River Recreation Area, Michigan. Means within a single life stage and year followed by different letters are significantly different at P < 0.05. Table modified from MacDonald et al. (2019) [280].

Life stage	Year	Restored***			Nonrestored,	
		Untreated	Burned	Hand pulled	Hand pulled	untreated
					and burned	
Seed bank	2015	231 (71)ab	137 (62)abc	73.4 (28.8)bc	31.4 (22.6)c	472 (112)a
	2016	52.4 (36.2)	10.5 (10.5)	115 (104)	10.5 (10.5)	178 (91)
Seedlings	2015	18.0 (4.5)b	22.3 (9.9)b	0.02 (0.01)c	0.01 (<0.01)c	118.8 (24.0)a
	2016	4.9 (1.7)b	1.4 (0.7)b	0.00 (0.00)c	0.00 (0.00)c	35.1 (10.6)a
Juveniles	2015	12.7 (5.5)b	6.6 (2.1)b	0.04 (0.02)c	0.06 (0.02)c	30.0 (4.7)a
	2016	7.5 (2.5)b	8.1 (2.6)b	<0.01 (<0.01)c	0.01 (0.01)c	42.6 (14.5)a
Adults	2015	4.8 (1.5)b	1.4 (0.4)c	<0.01 (<0.01)d	0.01 (<0.01)d	12.9 (2.6)a
	2016	3.9 (1.0)b	2.2 (1.3)b	0.00 (0.00)c	0.00 (0.00)c	16.4 (4.0)a

\*The fire in 2012 occurred during "suboptimal weather conditions" and fire intensity and severity were low (plot temperatures during the burn ranged from <79 to 159 °C).

\*\*The fires in 2014, 2015, and 2016 occurred during "more optimal weather conditions" and "burning effects were more pronounced".

\*\*\*Plots in "restored" plant communities were mowed, treated with herbicide, and seeded with warmseason grasses in 2008 as described in MacDonald et al. (2013) [284] and Martin et al. (2014) [306].

### **Postfire Reproduction**

Fire that occurs at the time of flowering can reduce spotted knapweed reproduction. In Augusta, Michigan, annual spring prescribed fires for 3 years and two alternate-year spring prescribed fires reduced the percentage of adults that flowered by approximately 50%, while annual and alternate-year summer prescribed fires reduced flowering almost entirely in those populations during the burn year. Spring prescribed fires occurred before plants had bolted, while summer prescribed fires occurred when plants had begun flowering. Annual and alternate-year fall prescribed fires had no effect on flowering because fall prescribed fires occurred after adults had produced seeds. Because of the strong effect of burning on flowering, annual summer prescribed fires reduced total seed production in all years, although the reduction was not significant in 2003 (table 6). Alternate-year spring and summer prescribed fires reduced seed production in the year of the fire in 2001, but not in the two subsequent years. Fall prescribed fires had no effect on seed production and appeared to increase germination success of seeds by reducing litter [129,131].

# **Postfire Seed Banking**

Only two studies, which occurred at the Bass River Recreation Area, examined postfire spotted knapweed seed banks and both found densities tended to be lower in burned than unburned plots after low-intensity consecutive annual spring prescribed fires. In one study, mean spotted knapweed seed density in the upper 5 cm of soil in mid-July was lower on plots burned consecutively in spring for 3 years (52 seeds/m<sup>2</sup>) than in unburned plots (~200 seeds/m<sup>2</sup>), although the difference was not statistically significant [285]. In an adjacent area in another study, mean density of spotted knapweed in

the upper 5 cm of soil in April in restored, burned plots (10.5 seeds/m<sup>2</sup>) was lower than those in restored, untreated plots (52.4 seeds/m<sup>2</sup>) and nonrestored, untreated plots (178 seeds/m<sup>2</sup>) following 3 consecutive annual spring prescribed fires (2014, 2015, and 2016) and an additional prior prescribed fire (2012), although differences were not statistically significant [280] (table 9). Higher intensity fires than those in these studies may help reduce seed bank survival, but further study is needed [129].

#### **Postfire Seedling Establishment**

Spotted knapweed germination and seedling emergence are reduced after fire [3,131,282,517] (see Immediate Fire Effects), but fire is likely to create conditions that are favorable for spotted knapweed seedling establishment by increasing bare ground, reducing litter and vegetation, and increasing sunlight at the soil surface [129,284,438,543]. Dry conditions after fire are likely to reduce postfire spotted knapweed seedling establishment, while moist conditions are likely to increase it [69,285], but no published studies examined this. Limited published information indicates that if soil moisture is adequate then postfire site conditions are likely to be favorable to spotted knapweed seedling establishment [284]. Two studies found that early postfire seedling establishment is variable from year to year and may be low on both burned and unburned plots [280,284]. In restored tallgrass prairie at the Bass River Recreation Area, density of spotted knapweed seedlings was lower on burned than unburned plots in August following annual mid-spring (late April to late May) prescribed fire for the first 2 years of the 3-year study. During the third year, seedling density was low, but similar between burned ( $\approx 1$ seedling/m<sup>2</sup>) and unburned ( $\approx$ 2 seedlings/m<sup>2</sup>) plots [285] (table 8). In an adjacent study area, spotted knapweed seedling density was higher in mid-July on plots burned in early April 2012 (1.8 seedlings/m<sup>2</sup>) than unburned plots (0.9 seedlings/m<sup>2</sup>) [284]. Plots were burned again in 2014, 2015, and 2016. In 2016, spotted knapweed seedling densities were statistically similar between burned (1.4 seedlings/m<sup>2</sup>) and untreated control (4.9 seedlings/ $m^2$ ) plots [280] (table 9).

In a greenhouse study, burning of spotted knapweed in pots at two burn intensities reduced seedling establishment in three life stages relative to an unburned control (table 10). Life stage had a greater effect on seedling establishment than burn severity, with the greatest reduction occurring in 2-week-old seedlings. Reduced seedling establishment when burning occurred before germination was directly related to reduced germination of burned spotted knapweed seeds, while reduced seedling establishment when burning occurred at 1 and 2 weeks old was caused by the death of the burned seedlings. Seedlings that established after the burns in the pots with the 1- and 2-week old seedlings were almost entirely the result of postfire germination rather than survival of burned seedlings [282] (see Immediate Fire Effects).

Table 10—Mean number of spotted knapweed seedlings established/pot by three treatments and three life stages.

Pots with low-intensity fire had 0.28 oz of fuel/pot and pots with high-intensity fire had 0.56 oz of fuel/pot. Means not followed by the same letter are significantly different at P < 0.05. Table modified from MacDonald et al. (2001) [282].

Treatment	Life Stage			
	Before germination	One-week old	Two-week old	
	(seeds)	seedlings (cotyledon)	seedlings (primary leaf)	
Unburned control	16.5 (4.1) a	23.0 (7.6) a	17.0 (4.1) a	
Low-intensity fire	4.5 (3.9) b	1.0 (1.2) bc	0.8 (1.0) c	
High-intensity fire	3.8 (1.5) b	1.5 (0.6) bc	0.3 (0.5) c	

# FUEL CHARACTERISTICS

Spotted knapweed stems may remain erect for a year [240]. They have high amounts of silica that "thwart attempts at burning" [533]. They decompose at a similar rate as bluebunch wheatgrass [313]. Spotted knapweed moisture content declines throughout the summer [534] (table 11). Green spotted knapweed plants are too moist to carry fire, but dried spotted knapweed plants can provide fuel [403]. Litter is lower in spotted knapweed communities compared with native grassland communities [145]. Spotted knapweed does not carry fire as readily as grasses in invaded communities, and dense spotted knapweed populations may have insufficient grass to carry fire [2,129,310,384,403,454,549] (Prescribed Fire, Fuels, and Fire Behavior). For example, in tallgrass prairie in Michigan, annual spring prescribed fires were used to reduce spotted knapweed density at sites with low to moderate spotted knapweed density and sufficient fine fuels to carry a fire when humidity and dead fine fuel moisture were "as low as possible". However, annual spring prescribed fires could not be used to reduce spotted knapweed density at sites with dense spotted knapweed (>60 rosettes/m<sup>2</sup>) due to a lack of adequate fine fuel to carry the fires [310].

Table 11—Seasonal moisture data for spotted knapweed collected on a south-facing slope in the Missoula Valley, Montana, in 1986.

Date	Mean moisture content	Development characteristics
	(% of dry weight)	
July 1	235	Flowerheads in dough stage. Grasses started drying.
July 9	210	Few flowers open. Grasses drying.
July 15	170	Approximately 20% of the flowers open. Grasses mostly dry.
August 1	120	80% of the flowers open. Few flowers (<3%) lost petals and
		dried. Lower spotted knapweed leaves turning yellow. Grasses
		mostly cured.
August 6	93	All flowers open. 5%–10% of flowers lost petals. Lower spotted
		knapweed leaves mostly dry.
August 20	45	Spotted knapweed plants look dry. Most leaves crumbly and
		yellow. Less than 10% of flowers retain petals.
August 27	30	Plants with any green leaves very rare. Less than 2% of flowers
		retain petals.

Table reproduced from Xanthopoulos (1986) [548].

Few studies provided information on spotted knapweed fuel loads. Near Helmville, Montana, an area with 13% spotted knapweed cover had 122 kg/ha of spotted knapweed and an area with 36% spotted knapweed cover had 295 kg/ha of spotted knapweed [499].

A fuel model for spotted knapweed and guidelines for prescribed burning in western Montana are available. Calculation of fuel load is based on spotted knapweed plant height, percentage of ground cover (old, standing plants and new plants), and litter depth and cover (including sparse grasses). The model was developed for early spring burns and is valid only under specific fine fuel loading conditions [548,549].

#### **FIRE REGIMES**

Spotted knapweed is most invasive in grasslands, semi-arid shrublands, woodlands, and open forests in the western, midwestern, and northeastern United States [91,99,101,178,262,273] (see Plant <u>Communities</u> and <u>General Distribution</u>). While it is unclear how fire regimes of invaded plant communities might affect or be affected by spotted knapweed populations, spotted knapweed fuels do not carry fire as well as grass fuels [2,129,310,384,403,454,549] (see Fuel Characteristics), and dense spotted knapweed populations may change the fuel characteristics of an invaded site formerly dominated by grasses and thus alter fire regime characteristics such as fire-return interval and fire severity [129,549]. To find fire regime information for plant communities in which spotted knapweed is invasive, enter "spotted knapweed" on the FEIS home page.

#### FIRE MANAGEMENT CONSIDERATIONS

### Fire as a Control Agent

Most published information about controlling spotted knapweed with prescribed fire comes from studies in forests in Montana [11,30] and British Columbia [204], tallgrass prairies and other warm-season grasslands in Michigan [129,201,280,283,284,285,306,312,384] and literature reviews (e.g., [124,125,259,421,437,438]). No published information was available regarding use of prescribed fire to control spotted knapweed in other regions or plant communities. The effectiveness of fire for killing spotted knapweed and other invasive plants or reducing their population growth depends on the plant community and fire characteristics (season, intensity, severity, and frequency) [259,398,437].

**Forests:** Available information from Douglas-fir and ponderosa pine communities suggests that spotted knapweed abundance may increase after some spring and fall prescribed fires (e.g., [<u>11,343</u>]); however, data are insufficient for drawing firm conclusions regarding prescribed fire effects on spotted knapweed in forests (see <u>Forests</u>).

**Tallgrass Prairies and Other Warm-season Grasslands:** In tallgrass prairies and other warm-season grasslands, low-intensity fires do not reach temperatures necessary to kill spotted knapweed seeds in the seed bank [280,285]. High-intensity fires may help reduce seed bank survival, but further study is needed [129] (see <u>Postfire Seed Banking</u>). If soil moisture is adequate, and the fire is of low intensity and severity, then postfire site conditions are likely to be favorable for spotted knapweed seedling establishment [284] (see <u>Postfire Seedling Establishment</u>). Consecutive annual prescribed fires (or some other follow-up treatments) are then needed to prevent subsequent seed production and thus reduce spotted knapweed populations in the long term [129] (see <u>Prescribed Fire Frequency</u>). Fires are most effective for reducing spotted knapweed populations in summer by killing spotted knapweed plants before they produce seeds [129,131]. However, fires at this time may be less beneficial to warm-season

grasses than spring fires [247,285,306,384] (see <u>Prescribed Fire Timing and Severity</u>). Sufficient fuels may not be available to carry consecutive annual fires [2,129,310,384,403,454,549] (see <u>Prescribed Fire, Fuels, and Fire Behavior</u>). Revegetation may be necessary in areas where desirable plant populations are depleted [124,205,331,436,437,446,515] (see <u>Revegetation</u>). Prescribed fire may be most effective at reducing spotted knapweed populations when it is used in combination with other control methods [280] (see <u>Integrated Management with Fire</u>).

#### Prescribed Fire Timing, Intensity, and Severity

In tallgrass prairies and other warm-season grasslands, low- or high-intensity summer prescribed fires that occur during the flowering stage can reduce spotted knapweed abundance and population growth by reducing reproduction [129,131,384]. Prescribed fires in spring may also be effective if the fires are of high enough intensity and severity, but often spring fires are of too low of an intensity or severity to kill spotted knapweed plants and plants sprout and flower in the same growing season [129,280,284,285,384]. Pitman et al. (2019) concluded that summer burns are likely most effective for controlling spotted knapweed because reducing spotted knapweed abundance during the flowering stage in summer rather than in the rosette stage in spring reduces seed production and viability as well as abundance, thereby limiting reproductive capacity and contributions to the soil seed bank [384]. Prescribed fires that are not hot enough to eliminate all of the viable seed in the soil or to prevent root crowns from sprouting are unlikely to control spotted knapweed populations [259,398,437].

Summer burning, however, is a "nontraditional management option" in tallgrass prairies [129] as most burns are conducted when vegetation is dormant in early spring or late fall due to "operational ease" [285] and because fires in spring appear to favor growth and dominance of established warm-season grasses more so than summer burns [247,285,306,384]. While summer burns may be most effective for controlling spotted knapweed in tallgrass prairie and other warm-season grasslands [129,384], spring burns of high enough intensity and severity can help control spotted knapweed at least in the short-term [280,285]. In reconstructed mesic tallgrass prairie in Barry County, Michigan, cover and biomass of newly planted warm-season grasses were generally higher following experimental fires in mid-spring than in summer, although differences were negligible perhaps because plants were not given much time to establish before burning. Median spotted knapweed cover and biomass were reduced regardless of burn season (mid-spring or summer), although summer fires were more effective than spring fires at reducing spotted knapweed cover and biomass, overall [384] (table 7).

Increases in warm-season grass abundance and decreases in spotted knapweed abundance following spring burns in warm-season grasslands may not be long lasting. In restored warm-season grasslands at the Bass River Recreation Area, the biomass and dominance of established warm-season grasses tended to be higher and that of spotted knapweed tended to be lower on burned than unburned plots following annual mid-spring prescribed fire for the first 3 years of a 3-year study [285]. However, 8 years after the last fire, this trend was no longer apparent (table 8). Biomass and dominance of native warm-season grasses in burned plots tended to be lower than or similar to unburned plots, while that of spotted knapweed were similar between burned and unburned plots. The researchers suggest that "while burning effects did not persist through time, reinstituting burning at appropriate intervals would be feasible given the abundance of grassy fuel present and positive response of native grasses to burning" [283].

#### Prescribed Fire Frequency

Spotted knapweed seedlings emerge from surviving seeds in the soil seed bank the first growing season after prescribed fire, so spotted knapweed abundance may increase after a single fire [430]. To reduce spotted knapweed populations, it is critical to kill these emerging plants before they produce seeds, as they are likely to be highly productive due to decreased competition for resources [284] (see Postfire Seedling Establishment). Seed bank densities were reduced following consecutive annual low-intensity spring prescribed fire in restored warm-season grasslands at the Bass River Recreation Area, although not statistically so [280,285]. High-intensity fires may be more effective than low-intensity fires at reducing spotted knapweed seed bank densities. This suggest that multiple consecutive years of highintensity prescribed fire may help reduce the density of spotted knapweed seeds in the soil seed bank, although the density of seeds of native species may also be reduced. Further study on this topic is needed [129] (see Postfire Seed Banking). While frequent burning can reduce spotted knapweed populations, it is often difficult to get a burn to carry through dense spotted knapweed patches [2,129,310,384,403,454,549] (see Fuel Characteristics). In addition, spotted knapweed is likely to establish from any remaining seeds in the soil seed bank or from seeds dispersed from off-site sources after annual burning ceases (e.g., [283]) (see Plant Response to Fire). Therefore, follow-up monitoring and treatment of seedlings may be needed for several years after burning ceases to prevent reestablishment [456,465].

#### Prescribed Fire, Fuels, and Fire Behavior

Fire behavior is affected by fuel loading and spotted knapweed fuel loads vary among sites. Intense fires in spotted knapweed stands in western Montana grasslands have been observed under some conditions, and prescribed burning for fire hazard reduction in spotted knapweed stands may be considered [548]. Fuel models developed for dense spotted knapweed stands suggest that flame lengths between 20 and 120 cm are needed to carry fire in spotted knapweed stands for fire hazard reduction in spring in western Montana. Grass fuel models are recommended over spotted knapweed fuel models if associated grass cover is >40%. However, these models have been verified with few actual test burns in spotted knapweed stands [548,549].

Sufficient fuels are needed for prescribed burning to be effective at killing spotted knapweed plants, and fuels may be insufficient where grasses are lacking, such as in dense spotted knapweed stands [2,129,310,384,403,454,549] (see Fuel Characteristics). Therefore, prescribed fire is most effective on sites that have sufficient grasses [2,129]. In tallgrass prairie, prescribed fire may be best used in areas with moderate spotted knapweed cover. On high-productivity sites, spotted knapweed is typically too sparse. On low-productivity sites, where spotted knapweed is dense and grasses are sparse, treatments that target nonreproductive adults, such as intense spot burning (using a propane torch) or spot herbicide, may be the most effective way to reduce population growth [129]. Spot burning may need to be repeated 3 to 4 times during the growing season to kill sprouting spotted knapweed plants and care must be taken to avoid nontarget effects on desirable plants [310].

Prefire herbicides, hand pulling, or mowing can enhance the effectiveness of burning by increasing the amount of dried fine fuels [124,306,403]. For example, at the Bass River Recreation Area, both clopyralid application and hand pulling increased grassy fuel loads, which the researchers hypothesized could facilitate future burns [306]. Deferring livestock grazing may allow fuels to build up prior to burning [548].

#### **Integrated Management with Fire**

Information on integrated management of spotted knapweed with prescribed fire or after wildfire comes from one study in a ponderosa pine forest in Montana [385], two studies in bunchgrass steppes in western Montana [197,256] and northeastern Washington [430], and two studies in warm-season grasslands in Michigan [280,281,283,284,285,306]. Integrated management information from other plant communities is lacking. Most studies integrating fire are short term. Limited data from long-term revegetation studies indicate that integrating prescribed fire with other control methods may be more effective at reducing spotted knapweed abundance than prescribed fire alone at least in the short term (e.g., [280]). Table A6 lists studies about spotted knapweed's response to fire alone and in combination with other control methods.

### **Prescribed Fire and Herbicides**

Literature reviews suggest that prescribed fire can be used to stimulate germination of spotted knapweed seeds, and herbicide can then be used to kill these seedlings [124]. In addition, burning removes plant debris, exposing spotted knapweed plants so that they are better seen and herbicides have better contact with them [111,124,125,438,543]. However, a study in western Montana found that April prescribed burning had no effect on postfire herbicide effectiveness 12 months after treatments, probably because dry conditions following burning limited spring germination of spotted knapweed prior to herbicide application [69].

#### <u>Forests</u>

Herbicides have been used to successfully control spotted knapweed on burned areas in forests. About 2 years after a severe, stand-replacing August wildfire in a ponderosa pine forest in Lame Deer, Montana, cover and density of spotted knapweed were greater on burned, untreated plots (36.6% and 106 plants/m<sup>2</sup>, respectively) than on burned, picloram-treated plots (6.6%–12.2% and 34–54 plants/m<sup>2</sup>). Spotted knapweed cover and density were lower and desired grass cover was higher on both broadcast-sprayed (in October after the fire) and spot-sprayed (in May after the fire) plots. Species richness, cover and density of desired forbs, and cover of undesired forbs other than spotted knapweed (e.g., primarily annual mustards and Canada thistle) were lower in broadcast-sprayed than spot-sprayed plots. Spotted knapweed cover and density were not affected by seeding desired species (grasses and/or forbs) the October after the fire. The authors hypothesized that while seeded species established, they may not have been mature enough to affect spotted knapweed abundance in the short term [385].

#### Bunchgrass Steppe

Herbicide may be an important integrated management tool in bunchgrass steppe. A study that tested multiple control methods for spotted knapweed on a northeastern Washington rangeland that included prescribed fire, herbicide application, fertilization, cultivation, and seeding, reported in an abstract that "treatments which did not include herbicide generally yielded the greatest amount of weeds and least amount of forage" [430].

On bunchgrass winter range on the Lolo National Forest, Montana, picloram was applied in June after an April prescribed fire with the objective of improving habitat for elk. By July of the following year, weed biomass (primarily spotted knapweed with small amounts of common mullein and leafy spurge) was 95% lower than pretreatment levels, native forb biomass was 86% lower, and grass biomass was 714% higher [197,256]. Sites were retreated in posttreatment year 2. By August of posttreatment year 3, weed biomass was 88% lower than pretreatment levels, native forb biomass are 70% lower, and grass 70% lower, and grass 70% lower, and grass 70% lower.

biomass was 79% higher [256]. These results indicate that the picloram treatments intended to decrease nonnative forb biomass also decreased biomass of many native forbs such as common yarrow, but biomass of some native forbs and many grasses increased [197].

#### Warm-season Grasslands

Several publications report findings from two studies on spotted knapweed-invaded warm-season grassland sites at the Bass River Recreation Area, which used single and consecutive annual prescribed fires to maintain restored prairies (i.e., newly established native grasses) and control spotted knapweed 3 and 4 years after initial restoration treatments [280,281,283,284,285,306]. Restoration treatments included various combinations of mowing, herbicide application (clopyralid and glyphosate), tillage, soil amendment (sewage sludge) and seeding a mix of native warm-season grasses and forbs. For information about the effects of prescribed fires on these restored sites, see <u>Tallgrass Prairies and</u> <u>Warm-season Grasslands</u>.

# Prescribed Fire and Physical Control

Integrating hand pulling with prescribed fire may be more effective than prescribed fire alone, at least in the short-term. In restored native warm-season grasslands at the Bass River Recreation Area, hand-pulled and pulled-and-burned restored plots had lower spotted knapweed seedling, juvenile, and adult density than untreated, restored plots each year of the 2-year study. Seedling, juvenile, and adult densities were similar between burned and untreated restored plots each year of the study with the exception of adult density during 1 year [280] (table 9). Czarapata [101] recommended hand pulling or digging spotted knapweed plants after prescribed fires if the postfire spotted knapweed populations are small enough.

### **Prescribed Fire and Livestock Grazing**

Few studies examined integrating livestock grazing with prescribed fire to control spotted knapweed, but one study indicated that heavy livestock grazing of rangelands after fire and herbicide application may increase spotted knapweed spread. Carpenter (1986) found that spotted knapweed quickly reestablished on burned rangelands in Threemile, Montana, probably due in part from heavy livestock grazing during summer [69].

### **Prescribed Fire and Biological Controls**

Prescribed fire can be harmful to biological control insects, but the effects depend on the insect species and the severity and timing of the fire. In general, seedhead-feeding insect larvae are likely to be killed by fire that consumes the plant, while root-feeding larvae are able to survive fast-moving, low- or moderate-severity fires underground. If fire occurs when the biological control insects are in the adult stage, many, such as the flies and moths, can escape the fire by flying away. This is not the case for the weevils (*Bangansternus fausti, Larinus minutus, Larinus obtusus*, and *Cyphocleonus achates*), which do not fly [476,543]. One year after a high-severity summer wildfire on the Helena National Forest, Montana, *Agapeta zoegana*, a root-feeding biological control insect, occurred in 9 of the 11 roots sampled [476]. At six sites in Wisconsin and Minnesota, only one biological control insect present before March and April prescribed fires was absent in July: a seedhead-feeding insect, *Urophora quadrifasciata*. This indicated that it likely did not survive the fires. All other insects present on the site before the fires (*Agapeta zoegana, Cyphocleonus achates*, *Larinus minutus*, *Larinus obtusus*, and *Urophora affinis*) were present after the fires and abundance of each was similar between burned and unburned plots [114].

# **Preventing Postfire Establishment and Spread**

Spotted knapweed has the potential to establish and spread after fire (see <u>Plant Response to Fire</u>). If spotted knapweed was present on or near a site before fire, there is potential for its establishment and spread after fire. As a precaution, it is a good idea to survey surrounding areas for spotted knapweed plants that could disperse seeds onto burned areas.

Application of fire retardant, which contains highly concentrated nitrogen and phosphorus fertilizer, may decrease or increase spotted knapweed cover, depending in part on competition with associated vegetation. One year after a July wildfire in Missoula, Montana, nonnative perennial forb cover (primarily spotted knapweed and Dalmatian toadflax) on burned and unburned bunchgrass steppe was lower in areas where retardant was dropped than in areas where retardant was not dropped. On dropped sites, cover of nonnative annual grasses and forbs (primarily cheatgrass and tall tumblemustard) increased, while cover of native grasses and forbs decreased. Personal observations by the researchers indicated that these patterns remained evident 5 years after the fire. However, experimentally applied retardant in a greenhouse increased the total mass of spotted knapweed in pots by 1,886% compared with pots without retardant. Retardant application did not result in an increase in the total mass of spotted knapweed when spotted knapweed was grown with cheatgrass, bluebunch wheatgrass, or field sagewort relative to that of spotted knapweed grown alone, and retardant tended to decrease the overall competitive effect of spotted knapweed on these species. In contrast, retardant application resulted in an increase in the total mass of cheatgrass when cheatgrass was grown with spotted knapweed, bluebunch wheatgrass or field sagebrush, and retardant more than doubled the competitive effect of cheatgrass, overall. These results suggest that spotted knapweed may increase mass following retardant application in the field if competition with other species (such as cheatgrass) is lacking and that postretardant control of spotted knapweed may be important for reducing spotted knapweed postfire establishment and spread and maintaining native plant communities [147]. A study examining the effects of available nitrogen on spotted knapweed found that spotted knapweed biomass tended to increase with nitrogen amendment (see Plant Growth) and recommended that land managers prevent activities that increase plant available nitrogen, such as direct fertilization and burning, and establish desirable species that will sequester nitrogen released by disturbance to prevent spotted knapweed establishment and spread [293].

Construction of firelines can create avenues for spotted knapweed establishment and spread. Preliminary results from the Bitterroot National Forest following the 2000 fire season showed higher densities of spotted knapweed on a bulldozer-constructed fireline and exponentially decreasing spotted knapweed density with distance from the fireline (S. Sutherland, USFS, Missoula, Montana, personal communication cited in [<u>16</u>]). General recommendations for preventing postfire establishment and spread of invasive plants, including spotted knapweed, include the following:

- 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 patches 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: [15,47,161,513].

# **OTHER MANAGEMENT CONSIDERATIONS**

### Federal Legal Status

None

### **Other Status**

Spotted knapweed is listed as a noxious weed is many states. See the <u>PLANTS Database</u> for information on state-level legal status of spotted knapweed.

### IMPORTANCE TO WILDLIFE AND LIVESTOCK

Parts of spotted knapweed plants are eaten by small and large mammals, including livestock, birds, and arthropods. The importance of spotted knapweed to wildlife and livestock depends on the size and density of the spotted knapweed population, the availability of other forage plants, and season of use.

### Large Mammals and Livestock

Large mammals, such as elk, deer, and bighorn sheep, and livestock eat spotted knapweed [322,538,547], but spotted knapweed displaces native vegetation which can lead to reductions in elk and deer habitat and forage [25,267,538], and livestock forage [182,292,507,524]. Spotted knapweed was preferred by mule deer and elk over other plant species on sites with dense spotted knapweed. Mule deer consumed spotted knapweed seedheads from December through April, while elk consumed

spotted knapweed seedheads only during winter [267,538]. Use of spotted knapweed seedheads by cervids may increase during periods of snow cover as these are often available above the snow [322,547]. In the Gilpin Range, British Columbia, elk and deer ate spotted knapweed and diffuse knapweed rosettes in late fall and early winter, and again during spring green-up, and spotted knapweed and diffuse knapweed seedheads were the primary forage of California bighorn sheep when snow was deeper than 20 cm. As snow cover receded in January and February, knapweed rosettes were the largest component (80%) of bighorn sheep diets. Knapweed rosettes and bluegrass comprised 90% of mule deer and white-tailed deer diets in February and early March [322].

Several studies suggest large potential losses of elk range to spotted knapweed invasion; however, quantifying the effects of invasion on elk populations is complicated by their mobility [25]. Because of diet differences, spotted knapweed invasion is considered more detrimental to elk than to deer [267,538]. In the Bitterroot Valley in western Montana, spotted knapweed-dominated sites were rarely used by elk and mule deer [538], probably because cervid densities were relatively low and other forage was available [547]. However, on spotted knapweed-invaded bunchgrass range in the Selway-Bitterroot Wilderness, Idaho, elk, mule deer, and white-tailed deer used spotted knapweed-invaded range as much as or more than uninvaded bunchgrass range from December through April, when all cervid species ate spotted knapweed rosettes and seedheads. Seedhead consumption was greatest during periods of snow cover [547].

Although domestic sheep and domestic goats readily graze spotted knapweed (e.g., [96,97,266,351,353,390,484]), and it is considered good forage for livestock [541], available livestock forage may be reduced on spotted knapweed-invaded range [182,292]. In general, grazing of spotted knapweed by livestock is highest during spring and early summer when plants are green and actively growing in the rosette and bolting stages [148,174,258,411,499] (see Palatability and Nutritional Value). Grazing declines as spotted knapweed matures, and protein and digestibility decrease [148,174,242], although flower buds and seedheads may be grazed in late summer [96,97,173,195].

Grazing by cattle, domestic sheep and domestic goats has been used as a control method for spotted knapweed (e.g., [97,173,195,266,539,541]) (see Livestock Grazing).

### **Small Mammals**

North American deermice (hereafter, deermice) eat spotted knapweed seeds and larvae of *Urophora* spp. [367,373], gall-forming biological control insects that overwinter in spotted knapweed seedheads [543]. This can have cascading effects on plant and animal communities. *Urophora* spp. larvae provide an abundant and nutritious food subsidy for deermice in winter when food is typically less abundant, which may result in increased survival and population size of deermice, shifts in deermouse use of the landscape, and increased prevalence of hantavirus in deermouse populations in areas with spotted knapweed [359,368,371,374,375]. In addition, large deermouse populations could reduce recruitment of native plants through increased seed predation [373], and *Urophora* spp. populations may be reduced below a threshold to effectively control spotted knapweed [375].

#### Birds

Spotted knapweed invasion may have negative effects on bird populations. For example, chipping sparrows in spotted knapweed-invaded ponderosa pine-Douglas-fir savannas in western Montana, had

degraded food resources, lower fecundity, and reduced fidelity to breeding sites compared with uninvaded savannas [355,361]. See Arthropods for more information.

Birds eat spotted knapweed biological control insects. Near Missoula, Montana, black-capped chickadees forage for *Urophora* spp. larvae on spotted knapweed seedheads in open woodlands [<u>356</u>], and select spotted knapweed seedheads with high densities of *Urophora* spp. larvae [<u>486</u>].

## Arthropods

Spotted knapweed provides an important nectar source for many insects, including some that are threatened and endangered. However, because spotted knapweed attracts so many pollinators, it can act as a "magnet species", reducing pollinator visits to, and thus seed production of, native plants [23]. In Lake Michigan sand dune communities, for example, the mean number of floral visitors to sand dune thistle, a federally threatened species, was three times higher in plots without spotted knapweed than plots with spotted knapweed [23].

Butterflies are frequently observed using spotted knapweed flowers [27,198] (fig. 6), and spotted knapweed is a nectar source for the federally endangered Karner blue butterfly in Wisconsin [166] and New York [143].



Figure 6—Monarch butterfly on spotted knapweed. Photo by Caleb Slemmons, National Ecological Observatory Network, and courtesy of Bugwood.org.

Bees, especially honey bees and bumble bees, are frequent spotted knapweed flower visitors (e.g., [23,26,73,133,186,198,244,524]). In Montana, 37 pollinator taxa visited spotted knapweed flowers, of

which 9 were exclusive visitors to spotted knapweed. The nonnative honey bee, accounted for 22% of all visits to spotted knapweed flowers and rarely visited flowers of other species. Nearly 43% of pollinator groups observed visiting spotted knapweed were bumble bees, 2% were honey bees, 46% were other native bees, 5% were flies, 3% were butterflies, and the remainder were beetles and unknown insects [198]. In old fields in Michigan, spotted knapweed was the most heavily visited plant in terms of total bee visitation and bee species richness [73].

Although spotted knapweed-dominated stands provide important floral resources for many insects while spotted knapweed is flowering, availability of floral resources is restricted at other times of year [73,198]. In Montana, spotted knapweed had the highest number of pollinator taxa visiting of 15 native and nonnative plant taxa studied. This was attributed to spotted knapweed being a relatively late bloomer compared with associated plants. During peak flowering, spotted knapweed-dominated plots attracted more pollinators than plots without spotted knapweed. However, spotted knapweed-dominated plots supported fewer pollinators before spotted knapweed started flowering because they had few plants other than spotted knapweed [198]. Spotted knapweed-dominated old fields in Michigan had high floral resource levels during peak flowering, but contained very few floral resources otherwise, while adjacent old fields with greater forb diversity provided floral resources before, during, and after spotted knapweed flowering. As a result, adjacent old fields had greater season-long floral resource availability and greater season-total bee abundance, diversity, and species richness than spotted knapweed old fields [73].

Spotted knapweed seeds are harvested by ants [228,229,325], and ants can be important spotted knapweed seed dispersers [229] (see Seed Dispersal). Preferential dispersal by ants of spotted knapweed seeds compared with native seeds may facilitate its invasion into native plant communities [229]. In western Montana, total ant species richness was greater in ponderosa pine-Douglas-fir savannas invaded by spotted knapweed than those not invaded, and ant genera, Formica species groups, functional groups, and reproductive ants were more abundant in invaded than noninvaded sites [228]. In Michigan, along Lake Superior, ants were captured more often in areas with spotted knapweed than without [305].

Hansen et al. (2009) documented a shift in the composition of the ground beetle community in areas dominated by spotted knapweed in western Montana, finding fewer generalist predators and more omnivorous and specialist predators. The authors hypothesized that this shift was a function of changes in food availability, namely increases in spotted knapweed and Lepidoptera, which presumably were consumed by omnivorous and specialized beetles, respectively [175]. Changes in arthropod populations and communities following invasions can have subsequent effects on other native wildlife, including reptiles, small mammals, and birds that rely on arthropods as important food sources. For example, areas dominated by spotted knapweed in western Montana had fewer grasshoppers, which are a major food source for many insectivorous songbirds. Reductions in abundance of grasshoppers associated with spotted knapweed invasion were correlated with delayed nest initiation in chipping sparrows, as well as reductions in territory density, site fidelity, and rates of double-brooding [361].

Grasshoppers may consume spotted knapweed seedheads and biological control larvae in those seedheads [428].

Spotted knapweed provides taller, wider, and more structurally complex flowering stalks than most native forb species in western Montana, and such flowering stalks are readily used by native spiders, especially *Dictyna* spp. In western Montana, *Dictyna* predation on invertebrates increased  $\geq$ 89 fold in webs in spotted knapweed compared to webs in native common yarrow. Invertebrate prey of these spiders included adult *Urophora* spp., spotted knapweed biological control insects [368]. Predation on *Urophora* spp. by *Dictyna* spp. may reduce adult *Urophorus* spp. populations [369]

Spotted knapweed may be less attractive to native predator arthropods than native vegetation. In western Michigan, spotted knapweed was attractive to arthropod "natural enemies" at multiple sites but less so than co-blooming native species [154].

#### **Palatability and Nutritional Value**

#### Palatability

Spotted knapweed is less palatable to elk and deer than other vegetation most of the year, but when animal densities are high and food choices are limited, such as from late fall to early spring, elk and deer will eat it [322,538,547] and may even prefer it to other available vegetation on sites with dense spotted knapweed [538]. Observations by Cox [97] suggest that spotted knapweed is more palatable to domestic sheep than orchardgrass, timothy, quackgrass, Kentucky bluegrass, sainfoin, or bird's-foot trefoil. Rocky Mountain bighorn sheep also ate knapweed seedheads and rosettes throughout the year in the Robson/Syringa Park area, British Columbia, with peak use in winter [322].

Livestock prefer young, succulent spotted knapweed plants, especially when they are relatively more palatable than associated vegetation [148,195,437,499], but will consume it at all growth stages (e.g., [148,174,266,541]). Mature spotted knapweed flowering stems are fibrous, coarse, and spiny, which makes them less palatable than young plants [83,407,437,438,510], and stems may be avoided [351,352,353,407].

### **Nutritional Value**

Spotted knapweed has adequate nutritional value during the growing season to sustain wild and domestic ungulates [148,174,499]. Near Missoula, Montana, spotted knapweed harvested before flowering contained 6.2% to 18.2% crude protein content, 24.2% to 53.0% neutral detergent fiber, and 53.2% to 61.8% in vitro digestible dry matter content and provided 4,088 to 4,539 calories/gram of gross energy [242].

Nutritional values vary with season, plant part, age, and site, and decline over time [<u>148,174,231,352,547</u>]. Crude protein and nonstructural carbohydrates are most concentrated during the spring. Plants becomes more fibrous, with lower protein and carbohydrate levels, as stems mature over the summer [<u>242</u>]. Seedheads are less nutritious than rosettes, but may be available above the snow [<u>547</u>].

Spotted knapweed produces secondary compounds such as the bitter tasting sesquiterpene lactone, cnicin, as an herbivore defense. Secondary compounds are present in all spotted knapweed aboveground plant parts, but highest concentrations occur in leaves [241,278] at the rosette stage [148]. Individual spotted knapweed plants produce varying levels of secondary compounds in response to different plant neighbors [49]. These compounds can reduce palatability [541] and digestibility

[78,348,350] of spotted knapweed, although some studies were unable to correlate changes in cnicin levels to changes in the amount of spotted knapweed consumed by mule deer, white-tailed deer, elk [547], or domestic sheep [148].

# Cover Value

Spotted knapweed may provide cover for a variety of animals. At Fort Custer State Recreation Area, Michigan, eastern box turtles nested in an open areas dominated by big bluestem, spotted knapweed, and common mullein [<u>317</u>]. In Grand Sable Dunes, Michigan, plots with spotted knapweed had nearly double the mean number of mice captures/trap than plots without spotted knapweed. Plots with spotted knapweed had higher total vegetative cover than plots without spotted knapweed and the mean number of mice captures/plot was positively related with cover [<u>290</u>].

# **OTHER USES**

Spotted knapweed provides substantial pollen and nectar for domestic bees in interior British Columbia [524], the Intermountain West [239], and Michigan [133,154].

Spotted knapweed leaves may exhibit antimicrobial activity. Information about spotted knapweed antimicrobial activity is available in the following sources: [39,85,116,241,492,516]. The combination of antimicrobial activity and phytotoxicity could make the compound (±)-catechin found in its roots a useful antimicrobial and natural herbicide [516]. Kelsey and Locken [241] cite studies indicating that the compound cnicin found in aboveground plant parts has antimicrobial properties, as well as being active against some human carcinoma cells and L-1210 leukemia. An endopyte isolated from spotted knapweed plant tissues collected from Idaho exhibited antiproliferative activity against human cancer cell lines and strong antifungal efficacy [1].

Extracts from spotted knapweed leaves collected from Oregon exhibited activity against Formosan subterranean termites, a nonnative species in the southern Unite States, suggesting that it could be used as a natural product to control populations of this pest [<u>314</u>]

### IMPACTS AND INVASION SUCCESS

### **Impacts**

Spotted knapweed can occur in dense monocultures (fig. 7) (see Population Structure and Growth) that

- displace native plants and reduce native plant species cover [236], richness, diversity [14,145,198,236,305,307,357,382,506,508], biomass [299,300,404], reproduction [360,404], and recruitment [360] and alter aboveground net primary productivity [311] and native plant physiology [245];
- reduce wildlife and livestock habitat and forage [25,182,292,493,507];
- increase bare ground cover [<u>145,508</u>] and alter soil physical and chemical properties [<u>187,206,311,348,495,547</u>] and soil biota [<u>52,184,271,313,338,339,489</u>]; and
- increase surface water runoff and stream sedimentation [261].

### **Impacts on Native Plant Communities**

Spotted knapweed's distribution is broad but impacts on native plant communities appear to be greatest in the West (see <u>General Distribution</u>). In parts of the East, some observations suggest spotted knapweed is not as invasive as in the West. For example, field observations in a grassy bald in

Shenandoah National Park, Virginia, indicated that increasing spotted knapweed abundance was not associated with decreasing abundance or diversity of plant species [<u>397</u>].



Figure 7—A dense spotted knapweed population near Missoula, Montana. Photo by Norman E. Rees, USDA Agricultural Research Service - Retired, and courtesy of Bugwood.org.

Dense spotted knapweed stands can fragment rare and sensitive plant habitat throughout its distribution. Several rare and sensitive plant species are negatively affected by spotted knapweed invasion. For example, spotted knapweed establishment and spread may contribute to rapid sand dune stabilization, which can exclude plants such as sand dune thistle that are adapted to disturbance by sand movement [103] (see <u>Succession</u>). Spotted knapweed can also reduce pollinator visits to sand dune thistle [23] and has a strong negative effect on its establishment, survival, and flowering [392]. However, spotted knapweed abundance was not negatively correlated with abundance of sand dune thistle or Lake Huron tansy, another species of concern in Great Lakes sand dune habitats [156]. Spotted knapweed is also a threat to several rare and threatened species in the Rocky Mountains. At the Big Hole National Battlefield in southwestern Montana, spotted knapweed is a management concern in populations of Lemhi penstemon, a rare endemic forb found only in five counties of Idaho and Montana [475]. In Idaho, spotted knapweed is "well represented" at sites with Spaulding's silene, a federally threatened species [202]. Spotted knapweed occurrence reduced seed germination and seedling establishment of Mt. Sapphire rockcress, a sensitive species, in Ravalli County, Montana [272].

#### Impacts on Wildlife and Livestock

Spotted knapweed invasion and introduction of biological control insects can alter large mammal [402,493,538], small mammal [359,368,371,374,375], bird [355,361], and arthropod [154,175,228,305,361,368,428] composition and abundance, which can have cascading effects on native plant communities [23,361,370,373]. For more information, see Importance to Wildlife and Livestock.

Spotted knapweed is considered a serious threat to rangelands in the western United States. On Montana rangelands in 2018, spotted knapweed and diffuse knapweed were reported by livestock producers as causing the third largest reductions in livestock production after leafy spurge and Canada thistle [292].

#### Impacts on Soil Properties and Soil Biota

Spotted knapweed can alter soil physical and chemical properties [145,187,206,311,495], although some studies found that soil physical properties associated with spotted knapweed and native grasses are similar [454]. In western Montana, spotted knapweed appeared to have the ability to increase the availability of nitrogen [206,311], phosphorus [145,495,555], and potassium [145] in some soils and reduce the availability of nitrogen [145,187,206,300], phosphorus [187], potassium [187], and soil carbon [145,206] in others. At Lac Du Bois Grassland Provincial Park, British Columbia, all measured soil variables were found to be different between spotted knapweed and native grassland communities [145]. However, in six western Montana sites, near-surface soil properties were similar between long-established spotted knapweed sites with >50% spotted knapweed cover and nearby native grass-dominated sites with <10% spotted knapweed cover, suggesting that its persistence could not be explained by an ability to alter near-surface soil characteristics [454].

Spotted knapweed may alter the abundance, composition, and diversity of soil biota (including bacteria, endophytic fungi, AMF, insects, amoebae, protozoa, and nematodes) within its own rhizospere and that of neighboring native plants (e.g., [52,63,184,271,311,313,316,338,339,489]); however, results are not consistent. For example, a study in western Montana found that spotted knapweed communities supported a higher abundance and diversity of AMF than native plant communities [271], while another study in western Montana found lower AMF abundance and diversity in spotted knapweed communities than native plant communities [338]. Yet another study found little to no effect of spotted knapweed on soil biota composition [54]. Results likely depend in part on the composition of the initial soil biota community [208]. Soil biota, in turn, may influence spotted knapweed regeneration processes [13,63,64,180,340,395] (see Soil Biota).

#### Impacts on Runoff and Sedimentation

The water-holding capacity of the soil decreases as spotted knapweed taproots replace the interconnected network of native plant root systems [101]. Surface water runoff and stream sediment yield were 56% and 192% higher, respectively, and infiltration rates lower, for spotted knapweed-dominated sites compared to bunchgrass-dominated sites in Garrison, Montana. Bare ground was greater and water infiltration rates were lower on spotted knapweed sites than on bunchgrass sites [261].

#### **Invasion Success**

Spotted knapweed invasion can be slow and insidious or rapid and conspicuous [260]. Because of its broad distribution and the many plant communities that spotted knapweed occurs in, it is difficult to

generalize about factors contributing to its invasion success [74]. Spotted knapweed invasion success varies among sites in part due to differences in <u>site characteristics</u> (especially <u>climate</u>, <u>soils</u>, <u>disturbance</u>, and <u>land uses</u>) and the composition and structure of <u>plant</u> [132,397], <u>animal</u> [229,370,373], and <u>soil</u> [180,316,396] communities. Spotted knapweed invasion success also depends on levels of <u>precipitation</u> [410] as well as spotted knapweed <u>propagule pressure</u> [30,301,407]. Several characteristics of spotted knapweed contribute to its invasion success: <u>allelopathy</u>, <u>life history traits</u>, and <u>genetic diversity</u>. For more information on these topics, see the following sections and publications in <u>table A7</u> and <u>table A8</u>.

# Allelopathy

Spotted knapweed contains varying concentrations of phytotoxic secondary compounds in its roots and aboveground tissues, particularly sesquiterpene lactones such as (±)-catechin (e.g., [18,20]), cnicin (e.g., [241,350]), and (E)- $\beta$ -caryophyllene (e.g., [209]). Researchers have proposed that one or more of these allelopathic chemicals could contribute to spotted knapweed's invasion success in North America, many describing them as a "novel weapon" in spotted knapweed's introduced range for which native species lack defenses (e.g., [18,33,61,62,188,212,215,405,485]). However, the contribution of allelopathy to spotted knapweed's invasion success is debated (e.g., [274,384]) and many studies do not find support for allelopathy as a novel weapon (e.g., [35,85,116,117,384,531]). See these literature reviews for more information on allelopathy in general [115,215,388,496], and of spotted knapweed in particular [61,65], as well as the publications in table A7. Fire may indirectly reduce levels of allelopathic chemicals in soils [278,384] but further study is needed.

### **Life History Traits**

The invasion success of spotted knapweed in North America has been attributed to tertraploidy and life history traits, specifically its perennial polycarpic life cycle, high reproductive capacity, and establishment success relative to its noninvasive, diploid relatives. These characteristics are believed to have preadapted spotted knapweed to conditions in North America (e.g., [90,168,169,196,301,329,417,480,483,490]) and allowed for postintroduction morphological and phenological adaptations [168,169,170,171,196,329,406,491] and climatic niche shifts [44,46].

Prolific seed production [260,424,524] (see Seed Production and Predation), germination throughout the growing season [299,300,302] (see Germination and Seedling Emergence), early and deep root development [296] (see Plant Growth), and preferential seed dispersal of spotted knapweed relative to some native plants [229] (see Arthropods) may also contribute to competitive dominance of spotted knapweed at some sites.

### **Genetic Diversity**

Spotted knapweed in North America has relatively high genetic diversity [<u>303,418</u>] and reduced inbreeding depression [<u>419</u>] compared with noninvasive relatives in its native range, which may have contributed to spotted knapweed's invasion success in North America.

### **Plant Community Attributes**

Plant community attributes that contribute to site invasibility by spotted knapweed include

abiotic environmental conditions and resource availability (water and soil nutrients) and their effect on spotted knapweed, associated plants, and their interaction (e.g., [36,107,149,187,250,253,299,349,480,495]);

- biomass [550], productivity [66,260,410,480], and spatial aggregation [149,491] of plants in the invaded plant community;
- dominant species' identity and their ability to compete for resources with spotted knapweed [130,132,300,307,480];
- functional similarity between spotted knapweed and dominant species [128,218,386];
- species and functional group richness and diversity of plants in the invaded plant community [130,299,302,307,410,481,491];
- ecotypic (within species) diversity of associated plants [550];
- establishment order of spotted knapweed and associated plants [425];
- past experience of associated plants with the <u>allelopathic chemicals</u> produced by spotted knapweed [<u>140,153</u>] and their susceptibility to them;
- neighbor-dependent differences in spotted knapweed gene expression [51]; and
- litter cover [<u>130</u>,<u>260</u>].

### **Enemy Release**

Spotted knapweed's invasion success has been attributed to the absence of specialist and generalist enemies (e.g., herbivores, seed predators, and soil biota) in its introduced range that would have competed with spotted knapweed and limited its establishment and spread in its native range (i.e., the Enemy Release Hypothesis) (e.g., [13,32,50,150,189,230,298,373,406,423]). Support for this hypothesis has led to the introduction of insects and pathogens from spotted knapweed's native range into its introduced range [32,51,199,324] (see Biological Control).

#### Soil Biota

Soil biota in the introduced range can have a positive [13,180,316,340], negative [63,64,222,340,395,422,478], or no effect [301,422] on spotted knapweed germination, seedling emergence, seedling establishment, recruitment, growth (biomass), and reproduction, depending on methods used, species of soil biota, and growing conditions. They may also similarly affect associated vegetation. Negative effects of soil biota on associated vegetation and positive effects on spotted knapweed might increase spotted knapweed's ability to compete for resources [13,59,340]. In addition, differences in the abundance, composition, and diversity of specific soil biota resulting from spotted knapweed invasion [52,184,271,313,338,339,489] (see Impacts on Soil Properties and Soil Biota) could be a mechanism contributing to its invasion success via positive plant-soil feedbacks [339,340,489]. Composition and abundance of soil biota may be influenced by fire [76], so burning effects on soil biota may have cascading effects on spotted knapweed and native plants.

Among soil biota, AMF may be particularly influential in spotted knapweed's invasion success in the West. Effects of AMF may be direct or indirect and spotted knapweed, AMF, and neighboring plants may interact in complex ways [63,68,297]. Arbuscular mycorrhizal fungi may increase spotted knapweed growth in some cases (e.g., [68,180,396]) (see Plant Growth) and spotted knapweed can exploit resources of neighboring plants via AMF hyphal connections between plants [63,68,297,396,544,555], thus altering competitive interactions between spotted knapweed and neighboring plants. In the East, such as in sand dune systems in the northern Great Lakes region, spotted knapweed does not appear to take advantage of AMF networks to exploit resources of neighboring plants [132]. For more information, see these literature reviews: [208,544] and the publications in table A8.

#### **Historical Land Uses Changes**

LeJeune and Seastedt (2001) reviewed the literature on knapweed invasiveness in grasslands of the West and concluded that historical overgrazing by livestock, fire suppression, and atmospheric nitrogen deposition have contributed to changes in native grasslands that rendered them more susceptible to establishment and spread of spotted knapweed and other *Centaurea* species [270]. Spotted knapweed invasion success varies geographically, and historical land use differences between regions (e.g., in railroad network development) may have contributed to observed geographical differences [44] (see <u>Site Characteristics</u>).

#### PREVENTION

Preventing spotted knapweed invasion is the most ecologically and economically effective management strategy [110,437]. Minimizing soil disturbance and maintaining desirable vegetation, limiting spotted knapweed seed dispersal, and establishing a program for monitoring and early detection can help prevent its establishment, persistence, and spread. If disturbance cannot be avoided, establishing desirable species on disturbed areas as soon as possible may reduce spotted knapweed establishment and spread [110,124,508,509,513] (see Revegetation). Trained domestic dogs can outperform human surveyors in the detection of rare spotted knapweed plants and thus contribute to the early detection of new spotted knapweed invasions [159].

#### **Maintaining Desirable Vegetation**

Maintaining productivity and species diversity in native plant communities may be important for limiting invasibility by spotted knapweed (e.g., [66,130,260,299,302,307,410,480,481,491]) because spotted knapweed is less competitive than native species when native species are dense and shade it [222]. In addition, plant communities that include species that are functionally similar to spotted knapweed, such as native forbs, are more resistant to its establishment and spread [128,218,386] (see Plant Community Attributes). Because spotted knapweed seedling recruitment increases with increased propagule pressure [301], reducing spotted knapweed propagule pressure and increasing native species propagule pressure are important to reducing site invasibility and maintaining desirable vegetation.

Activities that increase bare ground and remove other vegetation without replacement with desirable species are not recommended because spotted knapweed cover is likely to increase in areas with bare ground and reduced cover of other plants [124,363,421] (see Seedling Establishment and Mortality and Succession). In addition, reducing spotted knapweed density without filling the empty niches with more desirable vegetation may encourage the proliferation of other nonnative invasive plants [331,547]. For example, spotted knapweed may be replaced by cheatgrass [354,358,446,450] or vice versa [205]. In Idaho, spotted knapweed and yellow starthistle replaced common St. Johnswort after the introduction of biological control agents reduced its populations [67].

Proper grazing management is essential to the maintenance of a competitive, desirable plant community that can slow spotted knapweed establishment and spread [124,182]. Greenhouse [216] and field [219] studies found that defoliating associated grasses may result in an increase in spotted knapweed growth, cover, and density. To minimize weed invasion, grazing systems should alter the season of use, rotate or combine livestock types and pastures, and allow grazed plants to recover before being regrazed. On severely degraded, spotted knapweed-invaded rangelands, revegetation and rest from livestock grazing are recommended until revegetated species have established and established

plants can tolerate grazing and resist weed invasion [<u>124,216,260</u>]. For more information, see <u>Livestock</u> <u>Grazing</u>.

## Limiting Spread

Spotted knapweed spread can be reduced by limiting seed dispersal, controlling established plants in transportation corridors, and by detecting and eradicating new populations when they are small. Spotted knapweed seed dispersal can be limited by restricting vehicle, human, and livestock travel from spotted knapweed populations to areas without spotted knapweed, especially after seeds have matured and plants have died. Washing the undercarriage of vehicles leaving areas with weeds is recommended [124,508,509,513]. Controlling established plants in transportation corridors (highways, roads, and trails) can help limit spotted knapweed spread [30,398]. Public awareness of the identity and characteristics of spotted knapweed, support of local weed management programs, and restrictions for using only certified weed-free seed and hay for livestock entering the backcountry can also help prevent seed dispersal [110,124,239,295,337,509,513,521]. Detecting new populations when they are small improves chances for eradication and preventing persistence and spread onto new sites. This may be achieved with regular monitoring of susceptible areas, such as areas near established populations and along roads [101,124,257,295]. When spotted knapweed plants are found, remove them immediately. Controlling spotted knapweed first in areas in the early stages of invasion and on the edges of established populations is recommended [101,146].

# CONTROL

Control of spotted knapweed requires preventing seed production, depleting the spotted knapweed soil seed bank, and <u>establishing</u> and <u>maintaining</u> desired vegetation. Treated areas must be monitored multiple times a year for many years, and any new plants killed [2,204,249,258,508].

The following sections include information about general control methods available for spotted knapweed, including <u>fire</u>, <u>physical and mechanical control</u>, <u>livestock grazing</u>, <u>biological control</u>, and <u>chemical control</u>. Deciding which control methods to use may be determined, in part, by spotted knapweed cover [2] (table 12).

Spotted	Hand pulling	Mowing	Herbicide	Fire	Tillage
knapweed cover					
<5%	Х			Х	
5%-15%	Х	Х	Х	Х	
15%-25%		Х	Х		Х
>35%			Х		Х

Table 12—Spotted knapweed control methods based on the cover of spotted knapweed. Table from Abella (2001) [2]:

Frid et al. (2013) used a model to evaluate alternative weed management strategies to control spotted knapweed and leafy spurge in three regions of Montana and concluded that

- in the absence of management, the area occupied by these species will continue to increase exponentially leading to substantial economic costs (see <u>Impacts</u>);
- 2) even though the costs of management actions are substantial, there is a net economic benefit associated with a broad range of management strategies;

- 3) strategies that prioritize targeting small, new patches consistently outperform strategies that target large, established patches; and
- inconsistent treatment and short-term delays can greatly reduce the economic and ecological benefits of management [<u>146</u>].

Combining methods is likely more effective than any method alone (see <u>Integrated Management</u>). <u>Table</u> <u>A9</u> provides information from studies on spotted knapweed's response to control treatments other than fire that were published from 1999 to 2021.

# <u>Fire</u>

For information on use of prescribed fire to control spotted knapweed, see <u>Fire Management</u> <u>Considerations</u>.

# **Physical and Mechanical Control**

Removal of, or damage to, spotted knapweed plants by physical or mechanical methods may offer some degree of spotted knapweed control depending on the timing and frequency of treatment, the condition of desired vegetation, and the degree of soil disturbance imposed by the treatment itself.

### **Digging and Hand Pulling**

Persistent and careful hand pulling can control spotted knapweed [124]. Hand pulling is feasible for scattered spotted knapweed plants, or for areas where other control methods are not feasible and sufficient labor is available. Repeated hand pulling is necessary during the growing season and over many years. Successful control has been reported when plants were pulled three times a year (spring, summer, and late summer) over a period of 5 years. It is important to remove the entire taproot (or as much as possible) with as little soil disturbance as possible. When soils are dry, it may be difficult to remove the tap root and this can lead to sprouting and rapid reestablishment.

Hand pulling spotted knapweed may reduce spotted knapweed seed production and seed bank density if timed correctly and repeated over several years, but results are inconsistent. The best timing for pulling is before plants produce viable seeds. Flowering plants should be bagged, removed from the site, and properly disposed of to make sure that seeds do not mature [101,111,124,437]. Near Kamloops, British Columbia, spotted knapweed density in once-pulled plots was higher than in nonpulled control plots. Individuals in pulled plots recently germinated from the seed bank. The researchers concluded that pulling spotted knapweed increases opportunity for seeds to germinate from the seed bank. Thus, follow-up treatment is required after pulling treatments to deplete the seed bank [204]. In Ottawa County, Michigan, spotted knapweed was pulled twice a year for 4 years in restored warm-season grasslands. Mean seed bank density on pulled plots was similar to that of nonpulled plots for the first 3 years. Only in the fourth year was seed bank density less in pulled (68 seeds/m<sup>2</sup>) than nonpulled (524 seeds/m<sup>2</sup>) plots [284]. However, in both the seventh and eighth years of consecutive pulling, mean seed bank density on pulled plots was similar to that of nonpulled plots [280] (table 9). In southwestern Montana, pulling spotted knapweed and spaying with picloram in late June similarly reduced spotted knapweed cover but native forb cover, cheatgrass cover, and total nonnative plant cover were higher in pulled than sprayed plots while native grass cover was higher in sprayed than pulled plots [450].

#### **Mowing and Cutting**

Mowing is not possible in areas that are too rocky or steep or in areas with desirable shrub species, and mowing typically doesn't kill spotted knapweed plants [111]. Mowed plants generally survive if mowed before flowering and can recover to set seed [28,139,324,365,469]. Mowing after seed set can disperse seeds [111]. Mowing at the flowering or seed-producing stage is usually late enough to prevent reflowering and reduce flowering, seed production, and density of seeds in the soil seed bank [28,48,139,433,469,524] (see Seed Production and Predation), as well as decrease spotted knapweed density [408,433]. Rinella et al. (2001) conducted a 3-year mowing study of 16 timing and frequency combinations at two sites in Montana and found that a single fall mowing when spotted knapweed was in the flowering or seed producing stage reduced its cover and adult density as much as any treatment consisting of repeated mowing. A single mowing at this stage decreased adult spotted knapweed density by 83% and 85% at the two sites [408]. Mowing is typically most effective where the plant community contains perennial grasses that resume growth after mowing [124].

#### Tilling

Spotted knapweed does not persist under annual cultivation, which is why it is not typically a cropland weed [<u>111,182,524</u>]. On wildlands or rangelands, tillage may reduce spotted knapweed biomass and cover [<u>441,443</u>]; however, it may also increase its spread because tillage reduces desirable vegetation and creates an ideal seed bed [<u>110,111,474</u>]. Tillage is more successful if followed by <u>revegetation</u> [<u>125,398,443</u>].

### **Integrating Physical and Mechanical Controls**

Combining physical and mechanical treatments with other control treatments, such as herbicides, may be more effective than physical and mechanical treatments alone [48,279,284]. Near Missoula, Montana, combining physical and mechanical treatments (mowing and hand pulling) and spraying herbicide was more effective at reducing spotted knapweed cover than mechanical treatments alone. Spotted knapweed cover in mowed and pulled plots were not different from control plots, while sprayed plots, sprayed and mowed, and sprayed and pulled plots had lower cover of spotted knapweed than controls [279]. In rough fescue grasslands in Waterton Lakes National Park, Alberta, mechanical treatment (i.e., hand pulling, digging, and bagging) was found to be "ecologically efficient" (i.e., had little impact on native plant communities) for the control of spotted knapweed in small areas, while aminopyralid application was considered "economically efficient" (i.e., had fewer people involved) for the control of spotted knapweed. The author recommended integrated management that combines these methods [232].

Mowing is not recommended where biological control insects are well established and serve as the primary control strategy [124], because mowing at the recommended time (flowering or seed-production stage) kills the larvae of the seedhead-feeding biological control insects and reduces the availability of and delays access to floral resources required by the insects [124,139,324,469].

### Livestock Grazing

Although grazing is not an effective eradication method, grazing can reduce spotted knapweed plant biomass, density, size, flowering stem density, seed production, and soil seed bank density after 3 to 6 consecutive years of targeted grazing [327,353,407,541]. However, livestock grazing can create conditions that favor spotted knapweed invasion (e.g., soil disturbance and damage to desired plants) [111,410] and increase the probability of spotted knapweed establishment and survival [407]. Livestock

can also disperse viable spotted knapweed seeds in their feces up to 7 days after consumption [437,521] (see <u>Seed Dispersal</u>).

Domestic sheep, cattle, and domestic goats will graze spotted knapweed [111], especially when it is green and relatively more palatable than associated vegetation. Livestock grazing is not effective for controlling spotted knapweed once it is mature and relatively unpalatable [195,437,499] (see Importance to Wildlife and Livestock). Cattle and domestic sheep can be conditioned (trained) to consume increased amounts of spotted knapweed, although conditioning may only be successful under certain conditions and may not be long lasting [124,501,535,536]. Because spring herbicide application seemed to improve spotted knapweed palatability for domestic sheep, combined grazing and herbicide application was more effective at reducing spotted knapweed density after 3 years than grazing or herbicide alone [440].

The timing, frequency, and severity of defoliation is critical to successful control of spotted knapweed [111,422,541]. Management guidelines from 2006 recommended intense domestic sheep and domestic goat grazing during the rosette or bolting stage and again in the bud stage to provide the best control in the western United States [541]. However, grazing spotted knapweed during the flowering stage may be particularly effective because domestic sheep graze more spotted knapweed [484] and eat fewer graminoids [499] during mid to late summer than earlier in the season [484], especially in moderately dense spotted knapweed stands [499]. Frequent or intense grazing is required because spotted knapweed can compensate for low to moderate levels of defoliation by reallocating growth from roots to above-ground foliage (e.g., [56,341,523,556]). Two consecutive years of domestic sheep grazing in May to early June and again in late summer on 16 ha in western Montana with dense spotted knapweed completely eliminated spotted knapweed seed production, and the domestic sheep were healthy [96,239]. Domestic sheep grazing when grasses are dormant can reduce potential negative impacts on associated grass species [353] and reduce density of very young spotted knapweed seedlings, thereby limiting seedling recruitment [110,437]. Sequential cattle and domestic sheep grazing may control spotted knapweed without overusing desirable graminoids, especially when spotted knapweed is grazed in the late bud to early flowering stages rather than in the bolting stage [195].

Although few studies have examined the effects of combining herbivory by livestock and biological control insects, the results of one study in northwestern Montana suggested that combining prescribed domestic sheep grazing and biological control insects is more effective at reducing seed production and adult plant density and preventing compensatory recruitment of spotted knapweed than biological control insects alone [327].

### **Biological Control**

A 2012 literature review about biological control of spotted knapweed describes 16 organisms that have been introduced and tested for spotted knapweed control: 13 insects, 2 fungi, and 1 mite, but only the insects have been released in the field. The insects consist of three types: flies, moths, and beetles [543]. Table 13 lists the 13 insects released for knapweed biological control. For identification keys, insect descriptions, and life-cycle characteristics see Coombs et al. [92], Harris [184], and Winston et al. [543].

Scientific name	Common name
Seedhead-feeding insects	· · · ·
Bangansternus fausti	broad-nosed knapweed seedhead weevil
Chaetorellia acrolophi	knapweed peacock fly
Larinus minutus	lesser knapweed flower weevil
Larinus obtusus	blunt knapweed flower weevil
Metzneria paucipunctella	spotted knapweed seedhead moth
Terellia virens	green clearwing fly, verdant seed fly
Urophora affinis	banded knapweed gall-fly
Urophora quadrifasciata	UV knapweed seedhead fly
Root-boring insects	
Agapeta zoegana	sulfur knapweed root moth
Cyphocleonus achates	knapweed root weevil
Pelochrista medullana*	gray-winged knapweed root moth
Pterolonche inspersa*	brown-winged knapweed root moth
Sphenoptera jugoslavica	bronze knapweed root borer

Table 13—Spotted knapweed biological control insects.

\*According to Winston et al. (2012), these insects were not established in the United States as of 2012 and no studies published from 1999 to 2021 indicated that these insects have established [543] (table A9).

Larvae of insects used to control spotted knapweed damage plants by feeding inside either seedheads or roots. With the exception of two of the seedhead weevils, *Larinus minutus* and *Larinus obtusus*, adult insects have little impact on plants. Adult *Larinus* spp. can substantially defoliate knapweed stems and weaken plants. The larvae of each seedhead-feeding insect prefers certain seedhead characteristics and stages of development such that larvae of more than one species can occupy a seedhead at one time [543]. These larvae reduce seed production (e.g., [181,248,249,336,394,427,455,466,468,471]) (see Seed Production and Predation) and thus seedbank densities (see Seed Banking) by damaging and eating seeds and receptacle tissue [543]. The larvae of all five species of root-feeding insects can be present in the root at the same time [543]. These larvae reduce biomass and plant height [93,94,463], flower and seed production [251,463], and plant survival [93,289,360] by feeding on the root's vascular tissue or cortex [543].



Figure 8—Spotted knapweed root weevil (*Cyphocleonus achates*). Photo by Laura Parsons, University of Idaho, PSES, and courtesy of Bugwood.org.

Biological control insects are unlikely to eliminate spotted knapweed populations [341,543], but they may reduce its abundance (e.g., [93,94,152,224,251,461,464,470,477]). However, some field studies did not find an effect of one or more biological control insects on spotted knapweed abundance (e.g., [72,86,327,336]) and a common garden study found that spotted knapweed populations can compensate for adult mortality caused by *Cyphocleonus achates* herbivory by increasing the number of rosettes growing to the adult stage, resulting in no net change in adult population size [360]. The efficacy of biological control insects on reducing spotted knapweed abundance depends on the type and combination of biological control insects, their density, and the length of time they have been established [42,72,251,288], as well as precipitation and site characteristics such as plant and patch size, soil type and nutrients, and plant community composition [42,87,89,288,304,360,376,553]. Biological control insects may be especially useful in integrated control programs by increasing the efficacy of other control methods by weakening plants and/or reducing seed output [250,288,327].

Biological control insects may interact with precipitation levels to reduce spotted knapweed populations [288,376]. Models predict declines in spotted knapweed population growth rates for below-average and average precipitation levels, but not above-average precipitation levels when biological control insect (*Larinus minutus, Cyphocleonus achates*, and *Urophora* spp.) effects were included in population matrix models. Without biological control insects, models predicted population declines only for below-average precipitation levels [288]. Story et al. (2006) monitored spotted knapweed at two sites in western Montana from 1993 to 2004, during which time plant density declined 99% and 77%, despite above-

average precipitation in 7 years of the study. The decline was attributed to reduced spotted knapweed survival resulting from the biological control insect, *Cyphocleonus achates* [461]. However, other studies found that the effects biological controls and precipitation are not additive. Instead, biological control populations are low when spotted knapweed populations are stressed by drought and biological control populations are high when environmental conditions are good for spotted knapweed [360,455].

Spotted knapweed biological controls have nontarget impacts that alter the function of plant and animal communities [92]. For example, spotted knapweed's competitive dominance over several native grass species may be strengthened by biological control agents [60,492] (but see [341]). Biological control insects also provide food for animals, which can alter food webs [371,372,375]. For more details, see Importance to Wildlife and Livestock.

Biological control of invasive species has a long history, and there are many important considerations to be made before implementing a biological control program. More information on biological control for spotted knapweed is available from these publications: [183,331,420,505,542] and the Weed Control Methods Handbook [504].

### **Chemical Control**

Herbicides may be effective in gaining initial control of spotted knapweed, but are rarely a complete or long-term solution to weed management [554]. Control with herbicides is temporary, as it does not change conditions that allowed invasion to occur in the first place [124]. For large populations of spotted knapweed, herbicides are more effective when incorporated into long-term management plans that include replacement of weeds with desirable species, careful land use management, and prevention of new invasions [55,124]. See the Weed Control Methods Handbook [504] for considerations on the use of herbicides in natural areas and detailed information on specific chemicals.

Herbicides can be used to prevent new seed production by killing the plant and depleting the soil seed bank. Application of selective herbicide in combination with reseeding desirable grasses can reduce spotted knapweed establishment if soil moisture is suitable (e.g., [210,294,409,439,441,443]) (see <u>Revegetation</u>). Many herbicides have been tested for controlling spotted knapweed, and their application, efficacy, and length of control depend on a number of factors including the soil residual activity of the herbicide, site characteristics (e.g., soils), weather, and the present and desired plant community [11]. See DiTomaso et al. (2013) for information on the use and efficacy of specific chemicals on spotted knapweed [111] as well as the publications in <u>table A9</u>.

Herbicides have been used successfully to reduce the density of spotted knapweed seeds in the soil seed bank, but repeated applications are needed [81,83,474]. For example, when seed production was controlled with herbicide treatments at two sites in Harlowton and Ovando, Montana, "heavily infested" with spotted knapweed, the spotted knapweed seed bank decreased by 72% to 81% after 15 months [81,83]. After 7 years, only 5% of the original seed bank remained [104,105].

Prescribed burning may increase the efficacy of herbicide [<u>111,124,125,438,543</u>] and stimulate spotted knapweed germination prior to herbicide application [<u>124</u>]. See <u>Fire Management Considerations</u> for more information.

Biological control insects may be used in combination with herbicides if herbicide applications are timed appropriately and conducted at rates that reduce the impact of the herbicide on biological control insects [223,309,464,467,514]. Herbicides combined with biological control insects may prove more cost effective than herbicides or insects alone if insects establish and maintain long-term control [48].

#### **Integrated Management**

The use of multiple control methods is important when implementing any weed management system [110], because multiple approaches can create a cumulative stress on target plants, and reduce their reproduction and spread. This is especially true for management of large spotted knapweed populations [125]. With combinations of treatments, timing is critical and must be customized to the plant community, present and desired, and to site conditions [121].

Integrated management includes a long-term commitment to replace weed-dominated plant communities with more desirable plant communities. Methods selected for control of spotted knapweed on a specific site are determined by the extent of the spotted knapweed population, effectiveness of the control techniques on spotted knapweed, land use objectives, environmental factors, and cost [2,444]. Sheley et al. (1996) suggest using a generalized objective such as developing an ecologically healthy plant community that is weed resistant and meets other land-use objectives such as livestock forage, wildlife habitat, or recreation [446]. A weed-resistant plant community is comprised of diverse species that occupy most of the niches [123]. Once the desired plant community is determined, an integrated weed management strategy can be developed to direct succession toward that community by identifying key mechanisms and processes controlling plant community dynamics (site availability, species availability, and species performance) and predicting plant community response to control measures [431]. Components of any integrated weed management program are sustained effort, constant evaluation, and adopting improved strategies [437]. Some examples of combined approaches are presented within the preceding sections and in <u>table A9</u>.

#### REVEGETATION

No matter what method is used to kill spotted knapweed plants (see <u>Control</u>), establishment or maintenance of desirable plants is needed for long-term control [<u>124,205,331,436,437,446,515</u>]. It is important to reduce spotted knapweed abundance prior to establishing desirable species [<u>124,439,443,474</u>], and follow-up treatments that prevent spotted knapweed emerging from the soil seed bank may be necessary to control knapweed while desirable plants are establishing [<u>70,129,429,456,465</u>].

Successful restoration of desirable vegetation in spotted knapweed-invaded communities varies with spotted knapweed abundance and patch size, site characteristics (litter cover, soils, topography, and climate), fire characteristics (timing, intensity, severity, and frequency), precipitation, site preparation method (fire, mechanical, or chemical treatments), revegetation method (species mixes, native versus nonnative materials, seeding rates, and seeding and planting techniques), posttreatment livestock grazing (timing and intensity), and other factors [124,145,443,474]. Most studies on revegetating spotted knapweed-invaded sites are short term. Limited data from long-term revegetation studies indicate that seeded desirable species sometimes persist and suppress spotted knapweed for long

periods (at least 9 or 15 years). Short-term data do not reliably predict if, when, or where seeded species will persist and suppress spotted knapweed [409].

Reducing spotted knapweed density without filling the empty niches with more desirable vegetation may encourage reestablishment of spotted knapweed or proliferation of other nonnative invasive plants [331,547] thus, revegetation is often necessary. Shade and litter provided by desired species reduces light available to spotted knapweed [429]. Seeding competitive, site-adapted species may be necessary in areas without residual populations of desirable plants [443]. Seeding desired grasses and forbs at high seeding rates, while limiting input of spotted knapweed seeds, may increase native species competitiveness with spotted knapweed [250,434,441,442,443,515]. Revegetation of grass species has been shown to inhibit reinvasion by spotted knapweed [210,515], and Muller-Scharer and Schroeder (1993) concluded that "establishment of a competitive grass cover is most effective for both the reduction of knapweed population has declined" [331]. However, species that are functionally similar to spotted knapweed, such as forbs, are most competitive for resources with spotted knapweed [128,218,386]. See <u>Plant Competition</u> for more information about competitive relationships with spotted knapweed.

Establishing and maintaining a diversity of plant functional groups enhances resistance to spotted knapweed invasion [386]. Therefore, seeding a combination of grasses and forbs with various growth forms and ecological traits may be more effective for long-term spotted knapweed control than seeding grasses or forbs alone. In a growth chamber study of competition between spotted knapweed, bluebunch wheatgrass, and Utah sweetvetch, Jacobs and Sheley (1999) concluded that maintaining native tap-rooted forbs along with grasses increases niche occupation and may be more effective in minimizing invasion by spotted knapweed than grasses alone [218].

Because a weed-resistant plant community is comprised of diverse species that occupy most of the above and below ground niches [218,302,446], seeding a variety of species may reduce susceptibility of restored sites to reinvasion by spotted knapweed [70,299,386,434]. In Montana, monocultures were substantially more invaded than mixed-species assemblages that received identical initial additions of spotted knapweed seeds [299]. In experimental plant assemblages that varied in native species (1–16 species) and/or functional richness (defined by rooting morphology and phenology; 1–5 functional groups), assemblages with lower species and functional diversity were more heavily invaded by spotted knapweed than assemblages with greater species and functional diversity even under high resource availability [302]. In experimental studies in Montana, plant assemblages with high species richness were less invaded by spotted knapweed than less diverse assemblages [299]. However, species richness may not consistently reduce spotted knapweed recruitment even when desirable species are niche differentiated [70].

Dominant species' identity and their ability to <u>compete</u> for resources with spotted knapweed plays an important role in determining invasibility of plant communities by spotted knapweed (e.g., [<u>130,132,300,307,429,480</u>]), so selecting species for seeding that are competitive with spotted knapweed is important to preventing its reinvasion. However, no single species will suppress spotted knapweed on all sites at all times [<u>125</u>]. Species that have a deeper root system are likely most competitive for resources with spotted knapweed [<u>71</u>]. Several studies found decreased abundance of spotted knapweed where nonnative caespitose or rhizomatous wheatgrasses (e.g., [<u>71,210,224,439</u>]),

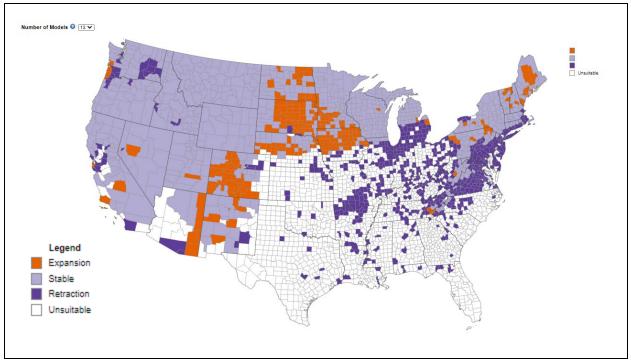
fescues (e.g., [185]) and bromes (e.g., [276]) were planted. However, some native bunchgrasses, such as bluebunch wheatgrass and Idaho fescue are less competitive than spotted knapweed, and do not prevent spotted knapweed invasion and growth [36,260,276,347]. Plant communities dominated by native, rhizomatous rough fescue or western wheatgrass appeared to be fairly resistant to spotted knapweed invasion [36,260,347]. Seeding nonnative species to revegetate spotted knapweed-invaded sites may reduce plant community diversity [112].

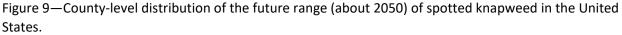
Spotted knapweed seedling emergence is positively correlated with number of spotted knapweed seeds added [455] and native plant seedling emergence is positively correlated with the number of native plant seeds added [442].

Establishment of native species in spotted knapweed communities may be increased with soil microbial amendments [246], but reduced by sludge amendments unless grasses are well established [281]. In Yakima County, Washington, seeding, sucrose addition (to increase the carbon:nitrogen ratio), and soil microbial amendments in spotted knapweed and diffuse knapweed communities appeared to create a soil environment more favorable for establishment and maintenance of native plant species than that in untreated controls [246].

#### MANAGEMENT UNDER A CHANGING CLIMATE

Ongoing and predicted increases in disturbance and elevated atmospheric carbon dioxide and temperature are likely to both expand and contract the distribution of spotted knapweed in parts of the United States and Canada [9,41,45,227] (table 14). Climate models based on 39,854 reported occurrences of spotted knapweed in the United States [9] predicted that by about 2050, spotted knapweed is likely to spread in the northern Great Plains, southern Rocky Mountains, and parts of the Northeast; and to retract from the Southeast [127] (fig. 9). Niche-based models that used distribution information from North America and Europe, predicted that by 2080, spotted knapweed is likely to spread in British Columbia and the Central Rocky Mountains [45]. Many areas in southern coastal Alaska are likely to become more suitable for spotted knapweed [227].





Climate change models from Allen et al. (2016) [9]. Map courtesy of EDDMaps [127], accessed 2021 March 11.

Bioclimatic envelope models suggest that climate change may enable spotted knapweed to expand to higher elevations in interior states (e.g., Montana, Wyoming, Colorado, and Utah), and retreat at lower elevations in western and eastern Montana [41]. If precipitation increases in Montana, this may increase vulnerability of plant communities to spotted knapweed invasion, although more diverse communities would be less susceptible to invasion than less diverse communities [302].

Spotted knapweed populations are likely to increase with increased carbon dioxide and nitrogen levels predicted for the end of the 21<sup>st</sup> century [277,557]. Because nitrogen addition may increase the growth and competitive ability of spotted knapweed more than native plants, potential increased atmospheric nitrogen deposition may increase the risk of spotted knapweed invasion [277].

Climate warming and nitrogen deposition may affect North American spotted knapweed populations differently than those in Europe [189]. For example, experimental warming of plots in a common garden sown with spotted knapweed with and without Kentucky bluegrass indicated that North American spotted knapweed plants were more tolerant to warming but had a weaker competitive ability than European plants under warming, even though their competitive ability was greater under ambient conditions. This suggests that warming could enable European but not North American spotted knapweed populations to become more invasive under future conditions [189], but the effects of future climate changes depend on the composition of plants in the community and the effects of warming on the associated plants as well as spotted knapweed [189,190,277,376].

Table 14—Publications from 1999 to 2021 that provide information on climate change effects on spotted knapweed.

Study location	Title	Reference
Geospatial models		
North America: throughout	Predicting current and future biological invasions: both native and invaded ranges matter	[ <u>45</u> ]
US: western	Climate change and plant invasions: Restoration opportunities ahead?	[ <u>41</u> ]
US: western	Out of the weeds? Reduced plant invasion risk with climate change in the continental United States	[ <u>9]</u>
AK: coastal	Cross-scale assessment of potential habitat shifts in a rapidly changing climate	[227]
Common garden, greenhouse, and	laboratory	
Common garden: spotted knapweed seeds collected from AR, MD, MT, VT, BC, Austria, France, Romania, and Ukraine	Simulated warming differentially affects the growth and competitive ability of <i>Centaurea maculosa</i> populations from home and introduced ranges	[ <u>189]</u>
Common garden: spotted knapweed seeds collected from MT	The tortoise and the hare: Reducing resource availability shifts competitive balance between plant species	[ <u>376</u> ]
Greenhouse: spotted knapweed seeds collected from AR, MD, MT, VT, and BC	Growth and competitive effects of <i>Centaurea stoebe</i> populations in response to simulated nitrogen deposition	[ <u>190</u> ]
Greenhouse: spotted knapweed seeds collected from invaded regions of North America	Enhanced shoot investment makes invasive plants exhibit growth advantages in high nitrogen conditions	[277]
Laboratory: spotted knapweed seeds collected from a commercial seed source	Evaluation of the growth response of six invasive species to past, present and future atmospheric carbon dioxide	[ <u>557]</u>

# APPENDIX

Table A1—Plant taxa mentioned in this review.

Table A2—Animal taxa mentioned in this review.

Table A3—Ecosystems, Associations, Cover Types, and BLM Regions where spotted knapweed likely occurs.

Table A4—Mean annual spotted knapweed seed production.

Table A5—Density and viability of spotted knapweed seeds collected in soil samples at various locations.

Table A6—Publications from 1999 to 2021 providing information on spotted knapweed's response to fire.

<u>Table A7</u>—Publications from 1999 to 2021 providing information on allelopathy of spotted knapweed. <u>Table A8</u>—Publications from 1999 to 2021 providing information on factors facilitating or inhibiting spotted knapweed invasion success in specific locations.

<u>Table A9</u>—Publications from 1999 to 2021 providing information on nonfire control treatment effects on spotted knapweed.

Common name	Scientific name
	Trees
balsam poplar	Populus balsamifera subsp. balsamifera
black cottonwood	Populus balsamifera subsp. trichocarpa
cedar	Thuja spp.
Douglas-fir	Pseudotsuga menziesii
Rocky Mountain Douglas-fir	Pseudotsuga menziesii var. glauca
grand fir	Abies grandis
hemlock	Tsuga spp.
jack pine	Pinus banksiana
juniper	Juniperus spp.
lodgepole pine	Pinus contorta
Rocky Mountain lodgepole pine	<u>Pinus contorta var. latifolia</u>
oak	Quercus spp.
pine	Pinus spp.
pinyon	Pinus spp.
ponderosa pine	Pinus ponderosa
Rocky Mountain ponderosa pine	Pinus ponderosa var. scopulorum
spruce	Picea spp.
subalpine fir	Abies lasiocarpa
western hemlock	Tsuga heterophylla
western juniper	Juniperus occidentalis
western redcedar	Thuja plicata
Shrubs	
big sagebrush	Artemisia tridentata
basin big sagebrush	Artemisia tridentata subsp. tridentata
mountain big sagebrush	Artemisia tridentata subsp. vaseyana
Wyoming big sagebrush	<u>Artemisia tridentata subsp. wyomingensis</u>
chokecherry	<u>Prunus virginiana</u>
dogwood	Cornus spp.
mallow ninebark	Physocarpus malvaceus
redosier dogwood	<u>Cornus sericea</u>
sagebrush	Artemisia spp.
saltbush	Atriplex spp.
sumac	Rhus spp.
threetip sagebrush	<u>Artemisia tripartita</u>
willow	Salix spp.
	Forbs
alfalfa*	<u>Medicago sativa</u>
annual mustards	Brassica spp.
arrowleaf balsamroot	<u>Balsamorhiza sagittata</u>
bird's-foot trefoil	Lotus spp.

Table A1—Plant taxa mentioned in this review. For further information on fire ecology of these taxa, follow the highlighted links to FEIS Species Reviews. Nonnative species are indicated with an asterisk.

bride's bonnet	Clintonia uniflora
Canada thistle*	Cirsium arvense
common mullein*	Verbascum thapsus
common St. Johnswort*	Hypericum perforatum
common yarrow	Achilleg millefolium
Dalmatian toadflax*	Linaria dalmatica
diffuse knapweed*	<u>Centaurea diffusa</u>
field sagewort	Artemisia campestris
knapweed*	Centaurea spp.
Lake Huron tansy	Tanacetum bipinnatum subsp. huronense
Lemhi penstemon	Penstemon lemhiensis
leafy spurge*	Euphorbia esula
Mt. Sapphire rockcress	Arabis fecunda
Russian-thistle*	Salsola kali
sainfoin*	Onobrychis viciifolia
sand dune thistle	Cirsium pitcheri
Spalding's silene	Silene spaldingii
sulphur cinquefoil	Potentilla recta
tall tumblemustard*	Sisymbrium altissimum
Utah sweetvetch	Hedysarum boreale subsp. boreale var. boreale
yellow starthistle*	Centaurea solstitialis
	Graminoids
big bluestem	Andropogon gerardii
bluebunch wheatgrass	Pseudoroegneria spicata
bluegrass	Poa spp.
cheatgrass*	Bromus tectorum
crested wheatgrass*	Agropyron cristatum
Idaho fescue	Festuca idahoensis
intermediate wheatgrass*	Thinopyrum intermedium
Johnsongrass*	Sorghum halepense
Kentucky bluegrass*	<u>Poa pratensis</u>
meadow fescue*	Schedonorus pratensis
medusahead*	Taeniatherum caput-medusae
mountain rush	Juncus balticus var. littoralis
needle and thread	Hesperostipa comata
orchardgrass*	Dactylis glomerata
purpletop	Tridens flavus
quackgrass*	<u>Elymus repens</u>
reed canarygrass*	Phalaris arundinacea
Richardson's needlegrass	Achnatherum richardsonii
rough fescue	Festuca altaica, F. campestris, F. hallii
Sandberg bluegrass	<u>Poa secunda</u>
sedge	Carex spp.
slender wheatgrass	<u>Elymus trachycaulus</u>
	· · · · · · · · · · · · · · · · · · ·

smooth brome*	Bromus inermis
timothy*	Phleum pratense
western needlegrass	Achnatherum occidentale
western wheatgrass	Pascopyron smithii
wheatgrass	Triticacea

Table A2—Wild animal taxa mentioned in this review. For further information on fire ecology of these taxa, follow the highlighted links to FEIS Species Reviews. Nonnative species are indicated with an asterisk.

Common name	Scientific name				
Arthropods					
ants	Formicidae				
bees	Hymenoptera				
beetles	Coleoptera				
bumble bees	Bombus spp.				
butterflies and moths	Lepidoptera				
cribellate araneomorph spiders	Dictyna spp.				
flies	Diptera				
Formosan subterranean termites*	Coptotermes formosanus				
grasshoppers	Orthoptera				
ground beetle	Carabidae				
half-moon hairstreak butterfly	Satyrium semiluna				
honey bee*	Apis mellifera				
Karner blue butterfly	Plebejus melissa samuelis				
	Reptiles				
eastern box turtle	Terrapene carolina				
	Birds				
black-capped chickadee	Poecile atricapillus				
chipping sparrow	Spizella passerina				
great horned owl	<u>Bubo virginianus</u>				
	Mammals				
bighorn sheep	Ovis canadensis				
California bighorn sheep	Ovis canadensis subsp. californiana				
Rocky Mountain bighorn sheep	Ovis canadensis subsp. canadensis				
deer	Odocoileus spp.				
elk	<u>Cervus elaphus</u>				
mule deer	Odocoileus hemionus				
North American deermouse	Peromyscus maniculatus				
white-tailed deer	Odocoileus virginianus				

	Ecosystems
FRES10	White-red-jack pine
FRES11	Spruce-fir
FRES13	Loblolly-shortleaf pine
FRES14	Oak-pine
FRES15	Oak-hickory
FRES17	Elm-ash-cottonwood
FRES18	Maple-beech-birch
FRES19	Aspen-birch
FRES20	Douglas-fir
FRES21	Ponderosa pine
FRES22	Western white pine
FRES23	Fir-spruce
FRES25	Larch
FRES26	Lodgepole pine
FRES28	Western hardwoods
FRES29	Sagebrush
FRES34	Chaparral-mountain shrub
FRES35	Pinyon-juniper
FRES36	Mountain grasslands
FRES37	Mountain meadows
FRES38	Plains grasslands
FRES39	Prairie
FRES42	Annual grasslands [151]
	Kuchler Plant Associations
К005	Mixed conifer forest
К008	Lodgepole pine-subalpine forest
K010	Ponderosa shrub forest
K011	Western ponderosa forest
K012	Douglas-fir forest
К013	Cedar-hemlock-pine forest
КО14	Grand fir-Douglas-fir forest
К015	Western spruce-fir forest
К016	Eastern ponderosa forest
КО17	Black Hills pine forest
КО18	Pine-Douglas-fir forest
КО19	Arizona pine forest
К022	Great Basin pine forest
К023	Juniper-pinyon woodland
K024	Juniper steppe woodland
K038	Great Basin sagebrush
K047	Fescue-oatgrass

Table A3—Ecosystems, Associations, Cover Types and BLM Regions where spotted knapweed likely occurs.

K048	California steppe			
K050	Fescue-wheatgrass			
K051	Wheatgrass-bluegrass			
K055	Sagebrush steppe			
K056	Wheatgrass-needlegrass shrubsteppe			
K063	Foothills prairie			
K064	Grama-needlegrass-wheatgrass			
K066	Wheatgrass-needlegrass			
К067	Wheatgrass-bluestem-needlegrass			
K068	Wheatgrass-grama-buffalo grass			
K074	Bluestem prairie			
K075	Nebraska Sandhills prairie			
K081	Oak savanna			
K082	Mosaic of K074 and K100			
K095	Great Lakes pine forest			
K100	Oak-hickory forest			
K104	Appalachian oak forest			
K106	Northern hardwoods			
K109	Transition between K104 and K106 [254]			
	SAF Forest Cover Types			
1	Jack pine			
14	Northern pin oak			
15	Red pine			
16	Aspen			
20	White pine-northern red oak-red maple			
21	Eastern white pine			
42	Bur oak			
43	Bear oak			
44	Chestnut oak			
50	Black locust			
51	White pine-chestnut oak			
52	White oak-black oak-northern red oak			
53	White oak			
55	Northern red oak			
64	Sassafras-persimmon			
109	Hawthorn			
206	Engelmann spruce-subalpine fir			
210	Interior Douglas-fir			
211	White fir			
212	Western larch			
213	Grand fir			
215	Western white pine			
217	A			
217	Aspen Lodgepole pine			

220	Rocky Mountain juniper
222	Black cottonwood-willow
224	Western hemlock
227	Western redcedar-western hemlock
228	Western redcedar Western hennoek
229	Pacific Douglas-fir
233	Oregon white oak
235	Cottonwood-willow
236	Bur oak
237	Interior ponderosa pine
238	Western juniper
239	Pinyon-juniper
243	Sierra Nevada mixed conifer
244	Pacific ponderosa pine-Douglas-fir
245	Pacific ponderosa pine Bodgids in
249	Canyon live oak
250	Blue oak-foothills pine [134]
250	SRM Rangeland Cover Types
101	Bluebunch wheatgrass
102	Idaho fescue
102	Antelope bitterbrush-bluebunch wheatgrass
105	Antelope bitterbrush-Idaho fescue
105	Bluegrass scabland
107	Western juniper/big sagebrush/bluebunch wheatgrass
109	Ponderosa pine shrubland
110	Ponderosa pine-grassland
210	Bitterbrush
215	Valley grassland
216	Montane meadows
301	Bluebunch wheatgrass-blue grama
302	Bluebunch wheatgrass-Sandberg bluegrass
303	Bluebunch wheatgrass-western wheatgrass
304	Idaho fescue-bluebunch wheatgrass
305	Idaho fescue-Richardson needlegrass
306	Idaho fescue-slender wheatgrass
307	Idaho fescue-threadleaf sedge
308	Idaho fescue-tufted hairgrass
309	Idaho fescue-western wheatgrass
310	Needle-and-thread-blue grama
311	Rough fescue-bluebunch wheatgrass-mentioned in this one
312	Rough fescue-Idaho fescue
314	Big sagebrush-bluebunch wheatgrass
315	Big sagebrush-Idaho fescue
· · · · ·	

317	Bitterbrush-bluebunch wheatgrass
318	Bitterbrush-Idaho fescue
319	Bitterbrush-rough fescue
320	Black sagebrush-bluebunch wheatgrass
321	Black sagebrush-Idaho fescue
322	Curlleaf mountain-mahogany-bluebunch wheatgrass
323	Shrubby cinquefoil-rough fescue
324	Threetip sagebrush-Idaho fescue
401	Basin big sagebrush
402	Mountain big sagebrush
403	Wyoming big sagebrush
404	Threetip sagebrush
405	Black sagebrush
406	Low sagebrush
407	Stiff sagebrush
408	Other sagebrush types
409	Tall forb
411	Aspen woodland
412	Juniper-pinyon woodland
413	Gambel oak
420	Snowbrush
421	Chokecherry-serviceberry-rose
422	Riparian
504	Juniper-pinyon pine woodland
601	Bluestem prairie
602	Bluestem-prairie sandreed
603	Prairie sandreed-needlegrass
607	Wheatgrass-needlegrass
608	Wheatgrass-grama-needlegrass
609	Wheatgrass-grama
610	Wheatgrass
612	Sagebrush-grass
613	Fescue grassland
614	Crested wheatgrass
615	Wheatgrass-saltgrass-grama [448]

Table A4—Mean (unless otherwise noted) annual spotted knapweed seed production at specific locations in the United States. Data included only for sites without biological control insects.

	included only for site		0		
Location; site type(s)	Seedheads/stem (unless otherwise noted)	Seeds/ seedhead	Seeds/plant	Seeds/m²	Reference(s)
Arkansas					
Greenland and Fayetteville; 2 fields sites with dense, continuous spotted knapweed	not reported	14.44 and 15.60	not reported	not reported	[108]
Washington County; a field dominated by spotted knapweed	not reported	≈3.6	not reported	not reported	[324]
Colorado					
Boulder; riparian meadow	not reported	≈3.5	not reported	not reported	[427]
Boulder; riparian meadow	not reported	7.7 and 13.9	not reported	not reported	[248]
Boulder; riparian meadow	not reported	5.37 and 6.24	not reported	not reported	[ <u>394]</u>
Idaho					
Athol; ungrazed rangeland	4.9 and 6.0	29.1 and 32.9	161.2 and 174.6	8,800 and 9,600	
Chilco; pasture	8.0, 9.3, 9.3, and 12.0	24.4, 29.4, 35.0, and 36.7	235.2, 292.8, 325.5, and 341.3	3,300, 7,200, 8,600, and 10,200	
Garwood; second- growth forest	7.4, 8.6, 12.6, and 21.7	24.4, 25.6, 30.3, and 32.1	220.2, 237.5, 381.78, and 525.1	10,400, 10,700, 15,700, and 19,300	[424]
Segal; disturbed forest	17.9, 25.8, and 37.3	27.5, 33.7, and 37.2	603.2, 709.5, and 1,387.6	31,100, 70,300, and 90,200	
Michigan					
Near Augusta; second- growth deciduous forest mixed with small prairie and oak savanna remnants	not reported	not reported	not reported	590.0, 1,384.0, and 2,051.2	[129]

Montana					
Blackfoot-Clearwater Game Range; site dominated by spotted knapweed (40%-80%), rough fescue, and bluebunch wheatgrass	not reported	Average across both years: ≈21	not reported	Year of below- average precipitation: 4,205.2 Year of average	[ <u>455]</u>
				precipitation: 5,342.8	
Chouteau, Fergus, and Pondera counties; dense spotted knapweed stands	not reported	2.23, 3.15, and 4.63	not reported	not reported	[451]
Corvallis; common garden	734.2 and 885.2	not reported	not reported	not reported	[ <u>93]</u>
Corvallis; old field dominated by spotted knapweed (59%)	5.2 and 5.5	not reported	7.6 and 11.8	not reported	[ <u>472]</u>
Corvallis; sites not described	not reported	1.4, 3.9, 14.4, 19.2, 30.4, and 32.9	not reported	365.5, 687.6, and 12,732	[471]
Missoula; sites not described	not reported	0.8, 2.0, 12.9, 16.5, 19.6, and 25.3	not reported	116.9, 143.0, 13,675	[4/1]
Glacier National Park; spotted knapweed dominated shortgrass prairie	4.7 and 4.8	23.5 and 29.1	not reported	8,060 and 8,460	[ <u>508]</u>
Glacier National Park; roadside ditch	5.2 and 16.9	25.4 and 28.5	not reported	26,290 and 37,340	
Milltown; site dominated by spotted knapweed	not reported	24.5	not reported	not reported	[186]
Missoula; common garden	not reported	not reported	Average precipitation: ≈240	not reported	[260]
	not reported	not reported	Below-average precipitation: ≈230	not reported	[360]

Stevensville, Lee Metcalf National Wildlife Refuge; spotted knapweed stand	not reported	≈17 and ≈18	not reported	not reported	[ <u>468]</u>	
Unknown location; site not described	not reported	21.36, 26.10, 28.07, and 29.56 number of seeds/seedh ead	not reported	not reported	[ <u>466]</u>	
Tennessee						
Eastern; sites with >75% cover of spotted knapweed	not reported	7.94	not reported	not reported	[252]	
British Columbia						
Chase	not reported	26.6	not reported	36,070	[101]	
Near Kamloops	not reported	19.9	not reported	not reported	[181]	
Near Kamloops; rangeland	16.4 seedheads/plant	26.6	436	not reported	[[]] 4]	
Kamloops; irrigated sites	707 seedheads/plant	35.8	25,263	not reported	[524]	
Outside the US						
Greenhouse; pots containing one spotted knapweed rosette grown from seeds collected from Austria	not reported	not reported	1,412	not reported	[ <u>335,530]</u>	



Location and	Methods	Spotted	Average	Average number	Viability (%)	Reference
plant	Methous	knapweed	number of	of viable seeds/m <sup>2</sup>		Reference
community		abundance	seeds/m <sup>2</sup> (SE)	(SE)		
MI: Ottawa	Seeds collected	Not reported	438 (46)	Not reported	Not reported	[284]
County	from 5-cm deep	Notreported	458 (40)	Not reported	Not reported	[204]
county	soil cores					
	collected in					
	March before					
	spring					
	germination					
MT: near	Seeds collected	99 adult	51,850	3,825 (1,285)	7.3	[217]
Bozeman;	from 8-cm deep	plants/m <sup>2</sup>	(30,600)			
site 1 (1994)	soil cores					
MT: near	collected prior to	10 adult	47,000 (7,900)	34 (43)	0.7	
Bozeman;	seed dispersal.	plants/m <sup>2</sup>				
site 1 (1995)	Viability based					
MT: near	on tetrazolium	177 adult	60,690	8,466 (3,060)	13.9	
Bozeman;	tests.	plants/m <sup>2</sup>	(13,133)			
site 2 (1994)						-
MT: near		151 adult	60,350	646 (850)	1.1	
Bozeman;		plants/m <sup>2</sup>	(13,023)			
site 2 (1995)						[
MT: Teller	Seeds collected	0.3 (0.05)	23.6 (9.6)	Not reported	Not reported	[ <u>471]</u>
Wildlife Refuge near	from 4.4-cm	stems/m <sup>2</sup>				
Refuge near Corvallis	deep soil cores collected 2					
MT: near	months after	0 stems/m <sup>2</sup>	5.9 (5.9)			
Corvallis	seed dispersal.	0 3(0113)111	5.5 (5.5)			
MT: Lee		0.3 (0.3)	47.2 (39.7)			
Metcalf		stems/m <sup>2</sup>				
National		,				
Wildlife						
Refuge near						
Stevensville						
MT: near		0 stems/m <sup>2</sup>	0			
Corvallis						
MT:		10.4 (3.0)	141.6 (34.7)			
Missoula		stems/m <sup>2</sup>				
MT: near		27.2 (6.8)	202.0 (32.3)			
Missoula		stems/m <sup>2</sup>				
MT: Skalkaho		24.0 (2.8)	595.9 (70.4)			
Pass, near		stems/m <sup>2</sup>				
Hamilton			402.0 (50.0)			
MT: Willow		35.7 (7.0)	182.9 (58.9)			
Creek near		stems/m <sup>2</sup>				
Corvallis						

MT: near		Not reported	758.9 (72.8)			
Harlowton						
MT: near Townsend		Not reported	7,677.8 (1,630.7)			
MT: Glacier National Park	Seeds collected from 10-cm deep soil cores collected in fall after seed dispersal. Viability determined by	40%–60% cover	Not reported	3,900	Not reported	[ <u>474]</u>
MT: Blackfeet Indian Reservation	germination in a greenhouse.			6,715		
MT: near Boulder	Seeds collected from 10-cm deep soil cores collected in October after seed dispersal. Viability determined by seed crush test and germination in a greenhouse	32% cover	5,848 (1,172)	468 (94) (seed crush test) 0 (germination)	8 (seed crush test) 0 (germination)	[250]
NY: McEnteer	Seeds collected from 5-cm deep soil cores in July.	Not reported	62.1 (35.6)	Not reported	Not reported	[321]
NY: Black Pond	Viability determined by germination in a	Not reported	184.8 (209.1)	Not reported	Not reported	
NY: Wehle	greenhouse.	Not reported	148.1 (90.7)	Not reported	Not reported	



Table A6—Publications from	1999 to 2021 providing information o	n spotted knapweed's response to fire.
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Study or collection location; plant	Title	Treatments investigated	Reference
community			
Forests			
MT: Bitterroot National Forest;	Spotted knapweed (Centaurea	Wildfires	[138]
Douglas-fir and subalpine fir	biebersteinii DC) response to forest		
forests	wildfires on the Bitterroot National		
	Forest		
MT: Lick Creek; Douglas-fir-	Eighty-eight years of change in a	Tree harvesting and May	[ <u>11</u> ]
ponderosa pine forest	managed ponderosa pine forest:	prescribed fires	
	Undergrowth response,		
	shelterwood cutting unit		
MT: Lame Deer; ponderosa	Managing spotted knapweed	Wildfire, herbicide	[ <u>385</u> ]
pine/chokecherry habitat type	( <i>Centaurea stoebe</i> )–infested	application (picloram),	
	rangeland after wildfire	and seeding with grasses	
		and/or forbs	
MT: Tenderfoot Creek	Roads impact the distribution of	Tree harvesting and 2	[ <u>30</u> ]
Experimental Forest; lodgepole	noxious weeds more than	years of consecutive	
pine forest	restoration treatments in a	annual prescribed fires	
	lodgepole pine forest in Montana,		
	U.S.A.		
MT, ID, and OR: 6 national forests	Response of six non-native invasive	Wildfires	[ <u>137</u> ]
in the northern Rocky Mountains;	species to wildfires in the Northern		
Douglas-fir-ponderosa pine, grand	Rocky Mountains, USA		
fir-western redcedar-western			
hemlock, and subalpine fir-			
lodgepole pine forest types		NATION AND A STREET AND A STREE	[204]
BC: near Kamloops; ponderosa	The effect of time-since-burning and	March prescribed fire and	[ <u>204</u> ]
pine and Douglas-fir forests in the	hand-pulling on the growth and	hand pulling	
ponderosa pine and bunchgrass	stem density of <i>Centaurea stoebe</i> and <i>Linaria dalmatica</i>		
Biogeoclimatic Zones			
Bunchgrass Steppes	Disturbanco, recourse pulses and	luluwildfiro	[20]
MT: Missoula; perennial	Disturbance, resource pulses and invasion: Short-term shifts in	July wildfire	[29]
bunchgrass steppe	competitive effects, not growth		
	responses, favour exotic annuals		
Tallgrass Prairies and Other Warm-s	•		
MI: Augusta; tallgrass prairie	Summer burns best for controlling	Annual and alternate-year	[121]
where spotted knapweed	spotted knapweed in prairie	April, July, and October	[ <u>131]</u>
comprised 6%-25% of the total	restoration experiment (Michigan)	experimental fires	
biomass			
טוטוומסס			

MI: Augusta; tallgrass prairie	Effects of timing of prescribed fire	Annual and alternate-year	[ <u>129</u> ]
where spotted knapweed	on the demography of an invasive	April, July, and October	
comprised 6%-25% of the total	plant, spotted knapweed Centaurea	experimental fires	
biomass	maculosa		
MI: Barry County; historically	Simulated fire season and	Two consecutive annual	[ <u>384]</u>
farmed, reconstructed tallgrass	temperature affect Centaurea	experimental and	
prairie with >20% spotted	stoebe control, native plant growth,	prescribed fires, followed	
knapweed cover	and soil (±)-catechin	by planting seeds and	
		seedlings of native	
		perennial grasses and	
		forbs	
MI: Bass River Recreation Area;	Mid-spring burning reduces spotted	Herbicide application	[ <u>285</u> ]
ruderal community dominated by	knapweed and increases native	(clopyralid and	
spotted knapweed historically	grasses during a Michigan	glyphosate), tillage, soil	
dominated by warm-season	experimental grassland	amendment, followed by	
grasses	establishment	seeding a mix of native	
		grasses and forbs. Three	
		years later plots were	
		burned under prescription	
		in late April to late May	
		each year for 3 years	
MI: Bass River Recreation Area;	Native warm-season grasses resist	Treatments as in [285].	[ <u>283]</u>
ruderal community dominated by	spotted knapweed resurgence	Plots were undisturbed for	
spotted knapweed historically		8 years after the third fire.	
dominated by warm-season			
grasses			
MI: Bass River Recreation Area;	Hand pulling following mowing and	Site preparation with	[ <u>284]</u>
ruderal community dominated by	herbicide treatments increases	mowing and/or herbicide	
spotted knapweed historically	control of spotted knapweed	application (clopyralid and	
dominated by warm-season	(Centaurea stoebe)	glyphosate), followed by	
grasses		seeding a mix of native	
		grasses and forbs. Hand-	
		pulling twice annually for	
		3 years beginning the year	
		after site preparation and	
		seeding. April prescribed	
		fire 4 years after site	
		preparation.	

MI: Bass River Recreation Area; ruderal community dominated by spotted knapweed historically dominated by warm-season grasses	Restoration of native-dominated plant communities on a <i>Centaurea</i> <i>stoebe</i> -infested site	Treatments as in [284]. Hand-pulling was continued twice each year for 8 years following that study. May prescribed fires were conducted 2, 3, and 4 years after the initial prescribed fire in that study.	[280]
MI: Bass River Recreation Area; ruderal community dominated by spotted knapweed historically dominated by warm-season grasses	Native plant establishment success influenced by spotted knapweed ( <i>Centaurea stoebe</i> ) control method	Treatments as in [284]	[ <u>306</u> ]
MI: Washtenaw County; tallgrass	Assessing plant community changes	April or November	[ <u>201</u> ]
prairie where spotted knapweed	over sixteen years of restoration in a	prescribed fire at 1- or 3-	
ranked 9 <sup>th</sup> most common species	remnant Michigan tallgrass prairie	year intervals	
Common garden/greenhouse/labor	atory		
Common garden: fallow field in	Native species richness buffers	A single August	[ <u>382</u> ]
Missoula, MT, planted with	invader impact in undisturbed but	experimental fire and	
experimental native bunchgrass	not disturbed grassland assemblages	experimental drought	
assemblages and seeded with			
locally collected spotted			
knapweed seeds			
Greenhouse: spotted knapweed	Intense burns may reduce spotted	Experimental fire with 4	[ <u>3</u> ]
seeds from Ottawa County, MI	knapweed germination	temperature levels and 3	
		levels of exposure	
Greenhouse: spotted knapweed	Invasive plant species and soil	Burned soils from wildfires	[ <u>192</u> , <u>193</u> ]
seeds and burned soils from	microbial response to wildfire burn		
mixed-conifer forest on the	severity in the Cascade Range of		
eastern slope of the Cascade	Oregon		
Range, Oregon			
Greenhouse: spotted knapweed	Pre- and post-germination burning	Seeding and experimental	[ <u>282</u> ]
seeds and soils from MI	reduces establishment of spotted	burns with 2 fuel loads	
	knapweed seedlings	(low and high) and 3 burn	
		times (immediately after	
		seeding, 1 week after	
		seeding, and 2 weeks after	
		seeding)	
Laboratory: spotted knapweed	Fire alters emergence of invasive	A single experimental fire	[ <u>517</u> ]
seeds from Miles City, MT	plant species from soil surface-		
	deposited seeds		

Table A7—Publications from 1999 to 2021 providing information on effects of spotted knapweed allelopathy.

Study or collection location	Title	Reference
Field studies		
MT: catechin in soils	A lack of evidence for an ecological role of the putative allelochemical (±)-catechin in spotted knapweed invasion success	[35]
MT, ID, and BC and laboratory: catechin in soils from MT, ID, and BC	Concentrations of the allelochemical (±)-catechin in <i>Centaurea maculosa</i> soils	[ <u>380]</u>
MT and Romania	Biogeographic differences in the effects of <i>Centaurea stoebe</i> on the soil nitrogen cycle: Novel weapons and soil microbes	[ <u>497]</u>
MT and Romania: catechin from commercial source	Root exudate is allelopathic in invaded community but not in native community: Field evidence for the novel weapons hypothesis	[ <u>498]</u>
MT and greenhouse: spotted knapweed seeds and plants from MT, catechin in from soils from MT	Insect herbivory stimulates allelopathic exudation by an invasive plant and the suppression of natives	[492]
MT and greenhouse: spotted knapweed seeds and catechin in soils from MT	Shoot herbivory on the invasive plant, <i>Centaurea maculosa</i> , does not reduce its competitive effects on conspecifics and natives	[ <u>341]</u>
MT and laboratory: spotted knapweed seeds from MT, catechin in soils from MT	Dual role for an allelochemical: (±)-catechin from <i>Centaurea</i> <i>maculosa</i> root exudates regulates conspecific seedling establishment	[ <u>381]</u>
VA and greenhouse: spotted knapweed seeds from VA	Comparing susceptibility of eastern and western US grasslands to competition and allelopathy from spotted knapweed ( <i>Centaurea stoebe</i> L. subsp. <i>micranthos</i> (Gugler) Hayek)	[ <u>397]</u>
BC and greenhouse: catechin from commercial source, spotted knapweed seeds from BC	Linking field based studies with greenhouse experiments: The impact of <i>Centaurea stoebe</i> (= <i>C. maculosa</i> ) in British Columbia grasslands	[307]
Palouse prairie in unknown location and greenhouse: spotted knapweed seeds from unknown source	The relative importance of allelopathy in interference: The effects of an invasive weed on a native bunchgrass	[405]
Common garden, greenhouse, and	laboratory	-
Common garden, greenhouse, and growth chamber: catechin from commercial source, spotted knapweeds seeds from MT	Oxalate contributes to the resistance of <i>Gaillardia grandiflora</i> and <i>Lupinus sericeus</i> to a phytotoxin produced by <i>Centaurea maculosa</i>	[531]
Greenhouse: catechin from commercial source, spotted knapweed seeds from MT	Soil ecological interactions of spotted knapweed and native plant species	[425]
Greenhouse: spotted knapweed seeds from commercial source	Root volatiles in plant–plant interactions II: Root volatiles alter root chemistry and plant–herbivore interactions of neighbouring plants	[209]

Greenhouse: spotted knapweed	Novel weapons and invasion: Biogeographic differences in the	[ <u>188</u> ]
seeds from 9 North American	competitive effects of Centaurea maculosa and its root exudate	
and 8 European populations	(±)-catechin	
Greenhouse: spotted knapweed	Natural selection for resistance to the allelopathic effects of	[62]
seeds and catechin from MT	invasive plants	
Greenhouse: spotted knapweed	Light intensity alters the allelopathic effects of an exotic invader	[79]
seeds from MT, soils from MT	<b>6</b> • • • • • • • • • • • • • • • • • • •	LJ
Greenhouse and laboratory:	Fungal endophyte increases the allelopathic effects of an	[12]
spotted knapweed seeds from a	invasive forb	,
greenhouse population and soils		
from MT		
Greenhouse and laboratory:	Catechin–metal interactions as a mechanism for conditional	[387]
catechin from a commercial	allelopathy by the invasive plant <i>Centaurea maculosa</i>	[ <u>507</u> ]
	aneiopathy by the invasive plant centulieu indculosu	
source Greenhouse and laboratory:	(±)-Catechin, a root exudate of the invasive Centaurea stoebe	[388]
catechin from a commercial		[300]
	Lam. (spotted knapweed) exhibits bacteriostatic activity against	
source, soils from MT and	multiple soil bacterial populations	
Romania		[05]
Laboratory: catechin from	(±)-Catechin: Chemical weapon, antioxidant, or stress regulator?	[ <u>85]</u>
commercial source		
Laboratory: catechin from	Chemical facilitation and induced pathogen resistance mediated	[ <u>391]</u>
commercial source	by a root-secreted phytotoxin	
Laboratory: catechin and 7,8-	The effects of flavonoid allelochemicals from knapweeds on	[ <u>8</u> ]
benzoflavone from commercial	legume-rhizobia candidates for restoration	
source		
Laboratory: catechin from a	A selective, sensitive, and rapid in-field assay for soil catechin,	[ <u>43</u> ]
commercial source, soils from	an allelochemical of Centaurea maculosa	
BC, MT, and Hungary		
Laboratory: catechin from a	New techniques and findings in the study of a candidate	[ <u>33</u> ]
commercial source, spotted	allelochemical implicated in invasion success	
knapweed seeds from CA, ID,		
MT, CO, and WI, soils from MT		
Laboratory: catechin from a	Structure-dependent phytotoxicity of catechins and other	[ <u>20]</u>
commercial source and spotted	flavonoids: Flavonoid conversions by cell-free protein extracts of	
knapweed seeds from CO	<i>Centaurea maculosa</i> (spotted knapweed) roots	
Laboratory: catechin from	Is (–)-catechin a novel weapon of spotted knapweed ( <i>Centaurea</i>	[116]
, commercial source, soils from	stoebe)?	
MT		
Laboratory: catechin from	Screening of grassland plants for restoration after spotted	[379]
commercial source, spotted	knapweed invasion	
knapweed seeds from MT		
Laboratory: catechin from a	Allelopathy and plant invasions: Traditional, congeneric, and	[214]
commercial source, soils from	bio-geographical approaches	L <u>——                                   </u>
MT, India, and Romania		

Laboratory: catechin from an	Phytotoxic effects of (±)-catechin in vitro, in soil, and in the field	[ <u>213]</u>
unknown source, soils from MT,		
India, and Romania		
Laboratory: catechin from an	Allelopathy and exotic plant invasion: From molecules and genes	[ <u>18</u> ];erratum:
unknown source, soils from	to species interactions	[ <u>19]</u>
North America and Europe		
Laboratory: spotted knapweed	Inference of allelopathy is complicated by effects of activated	[ <u>265</u> ]
seeds from CA	carbon on plant growth	
Laboratory: spotted knapweed	Elucidation of a diurnal pattern of catechin exudation by	<u>[488]</u>
seeds from MT	Centaurea stoebe	
Laboratory: spotted knapweed	Phytotoxic and antimicrobial activities of catechin derivatives	[ <u>516]</u>
seeds from MT		
Laboratory: spotted knapweed	Bioavailability of allelochemicals as affected by companion	[ <u>487]</u>
plants from MT	compounds in soil matrices	

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Study location; plant community	Title	Reference
Field studies		
ID: near Moscow; sites with long-term spotted knapweed populations	Nematodes associated with invasive spotted knapweed	[ <u>150</u> ]
MI: Kalamazoo County; old fields	Dominant species identity regulates invasibility of old-	[130]
with Ratamazoo County, old ficius	field plant communities	[ <u>130</u> ]
MT: Missoula; orchardgrass meadow	Neighboring plant influences on arbuscular mycorrhizal	[339]
	fungal community composition as assessed by T-RFLP	[333]
	analysis	
MT: near Bozeman and Helena; spotted	Advantages in water relations contribute to greater	[203]
knapweed monocultures	photosynthesis in Centaurea maculosa compared with	
	established grasses	
MT: near Missoula; Palouse prairie	Myrmecochory of the exotic plant, Centaurea	[229]
dominated by bluebunch wheatgrass and	maculosa: A potential mechanism enhancing	
Idaho fescue	invasiveness	
MT: Miles City; grasslands dominated by	Assessing invasiveness of exotic weeds outside their	[407]
western wheatgrass	current invasive range	
MT: near Bozeman; Idaho fescue-bluebunch	Grassland invader responses to realistic changes in	[410]
wheatgrass habitat type	native species richness	
MT and greenhouse: "harsh" site with	Shoot herbivory on the invasive plant, Centaurea	[341]
spotted knapweed and Idaho fescue, spotted	maculosa, does not reduce its competitive effects on	
knapweed seeds from unknown source, soils	conspecifics and natives	
from MT		
MT and greenhouse: near Helena, Belgrade,	Water use and water-use efficiency of the invasive	[37]
and Bozeman; semi-arid grasslands, spotted	Centaurea maculosa and three native grasses	
knapweed seeds from unknown source		
MT, Hungary, and Romania: native	Escape from competition: Neighbors reduce Centaurea	[66]
grasslands	stoebe performance at home but not away	
BC: near Kamloops; rough fescue-western	Is spotted knapweed ( <i>Centaurea stoebe</i> L.) patch size	[145]
needlegrass-Richardson's needlegrass	related to the effect on soil and vegetation properties?	
grasslands		
Slovakia and greenhouse: steppe; seeds from	Sympatric diploid and tetraploid cytotypes of Centaurea	[478]
Slovakia	stoebe s.l. do not differ in arbuscular mycorrhizal	
	communities and mycorrhizal growth response	
Common garden, greenhouse, and laboratory		1
Common garden: spotted knapweed seeds	Increased population growth rate in invasive polyploid	[168]
from 48 North American and 93 European	Centaurea stoebe in a common garden	
and eastern Asian populations	, , , , , , , , , , , , , , , , , , ,	
Common garden: spotted knapweeds seeds	Evidence for a combination of pre-adapted traits and	[196]
from 141 North American, European, and	rapid adaptive change in the invasive plant Centaurea	
Asian populations	stoebe	
Common garden: seeds from OR, MT,	Cytotype differences modulate eco-geographical	[170]
Germany, Hungary, and Ukraine	differentiation in the widespread plant <i>Centaurea</i>	
		1

Table A8—Publications from 1999 to 2021 about factors facilitating or inhibiting invasiveness of spotted knapweed.

Common garden: spotted knapweed seeds	An exotic invasive plant selects for increased	[140]
from MT	competitive tolerance, but not competitive	
	suppression, in a native grass	
Common garden: spotted knapweed seeds	Increased phenotypic plasticity to climate may have	[171]
from throughout North America, Europe,	boosted the invasion success of polyploid <i>Centaurea</i>	
and Asia	stoebe	
Common garden: spotted knapweed seeds	Increased seed survival and seedling emergence in a	[169]
from throughout North America, Europe,	polyploid plant invader	L
and Asia		
Common garden: spotted knapweed seeds	Ecotypic diversity of a dominant grassland species	[550]
from unknown source	resists exotic invasion	
Common garden and greenhouse: spotted	Effects of native species diversity and resource	[299]
knapweed seeds from MT	additions on invader impact	
Common garden and greenhouse: spotted	Field-based competitive impacts between invaders and	[300]
knapweed seeds from MT	natives at varying resource supply	
Common garden: spotted knapweed seeds	Biogeographic effects on early establishment of an	[480]
from Switzerland and Germany	invasive alien plant	
Common garden and greenhouse: spotted	Origin matters: Diversity affects the performance of	[481]
knapweed seeds from Switzerland and	alien invasive species but not of native species	
Germany		
Common garden and greenhouse: spotted	Soil fungi alter interactions between the invader	[63]
knapweed seeds and soils from MT	Centaurea maculosa and North American natives	
Common garden and greenhouse: spotted	Soil biota and exotic plant invasion	[64]
knapweed seeds from MT, soils from MT,		
France, and Italy		
Greenhouse: spotted knapweed seeds from	No evidence for trade-offs: Centaurea plants from	[406]
23 North American and 22 European	America are better competitors and defenders	
populations		
Greenhouse: spotted knapweed seeds from	Cytotypes of <i>Centaurea stoebe</i> found to differ in root	[ <u>88]</u>
Switzerland, Germany, Austria, Hungary, and	growth using growth pouches	
Romania		
Greenhouse: spotted knapweed seeds from	Fungal endophytes directly increase the competitive	[ <u>13</u> ]
greenhouse-grown plants and wild-grown	effects of an invasive forb	
plants in MT and Romania, spotted		
knapweed endophytes from ID and Hungary,		
soils from MT		
Greenhouse: spotted knapweed seeds from	Response of bluebunch wheatgrass to invasion:	[ <u>153</u> ]
MT	Differences in competitive ability among invader-	
	experienced and invader-naive populations	
Greenhouse: spotted knapweed seeds from	Soil ecological interactions of spotted knapweed and	[425]
MT	native plant species	
Greenhouse: spotted knapweed seeds from	Soil space and nutrients differentially promote the	[ <u>149</u> ]
MT	growth and competitive advantages of two invasive	
	plants	

<b>A</b>		10 4 53
Greenhouse: spotted knapweed seeds from	The role of the native soil community in the invasion	[ <u>316</u> ]
MT and soils from WA	ecology of spotted ( <i>Centaurea maculosa</i> auct. non	
	Lam.) and diffuse ( <i>Centaurea diffusa</i> Lam.) knapweed	
Greenhouse: spotted knapweed seeds from	Drought tolerance and plasticity in the invasive	[ <u>329</u> ]
OR, MT, WY, France. Germany, Ukraine,	knapweed Centaurea stoebe s.l. (Asteraceae): Effect of	
Slovakia, Serbia, and Bulgaria	populations stronger than those of cytotype and range	
Greenhouse: spotted knapweed seeds from	Complex interactions between spatial pattern of	[ <u>491]</u>
OR, MT, and Europe	resident species and invasiveness of newly arriving	
	species affect invasibility	
Greenhouse: spotted knapweed seeds from	Species-specific effects of polyploidisation and plant	[ <u>489</u> ]
OR, MT, and Europe	traits of Centaurea maculosa and Senecio inaequidens	
	on rhizosphere microorganisms	
Greenhouse: spotted knapweed seeds from	Polyploidy and invasion success: trait trade-offs in	<u>[490]</u>
OR, MT, Switzerland, Austria, Hungary, and	native and introduced cytotypes of two Asteraceae	
Ukraine	species	
Greenhouse: spotted knapweeds seeds from	A molecular approach to understanding plant-plant	[ <u>51</u> ]
MT and soils from CO and MT	interactions in the context of invasion biology	
Greenhouse: spotted knapweed seeds and	Impact of competition and mycorrhizal fungi on growth	[ <u>132</u> ]
soils from MI	of Centaurea stoebe, an invasive plant of sand dunes	
Greenhouse: spotted knapweed seeds from	Competition between cytotypes changes across a	[ <u>90]</u>
Switzerland, Germany, Slovakia, and	longitudinal gradient in <i>Centaurea stoebe</i> (Asteraceae)	
Hungary		
Greenhouse: spotted knapweed seeds from	Traits of the invasive Centaurea maculosa and two	[ <u>36</u> ]
unknown source	native grasses: Effect of N supply	
Greenhouse: spotted knapweed seeds from	Mycorrhizae indirectly enhance competitive effects of	[297]
unknown source, soils from MT	an invasive forb on a native grassland	
Greenhouse: spotted knapweed seeds from	Invasive plants escape from suppressive soil biota at	[ <u>298</u> ]
unknown source, soils from OR, WA, ID, MT,	regional scales	
ND, MI, ON, France, Germany, Austria, and		
Hungary		
Greenhouse: spotted knapweed seeds from	Belowground competition and response to defoliation	[422]
unknown source, soils from MT	of Centaurea maculosa and two native grasses	
Greenhouse: spotted knapweed seeds from	Host plant differences in arbuscular mycorrhizae: Extra	[ <u>522</u> ]
unknown source, soils from MT	radical hyphae differences between an invasive forb	
	and a native bunchgrass	
Greenhouse: spotted knapweed seeds from	Phosphorus uptake, not carbon transfer, explains	[555]
unknown source, soils from MT	arbuscular mycorrhizal enhancement of Centaurea	
	<i>maculosa</i> in the presence of native grassland species	
Greenhouse: spotted knapweed seeds and	Mycorrhizae transfer carbon from a native grass to an	[68]
soils from unknown source	invasive weed: Evidence from stable isotopes and	<u> </u>
	physiology	
Greenhouse and common garden: spotted	Herbivory on invasive exotic plants and their non-	[230]
knapweed seeds from an unknown source	invasive relatives	•

Greenhouse and laboratory: spotted knapweed seeds and plants from OR, MT, France, Switzerland, Germany, Austria, Hungary, and Ukraine	Plant origin and ploidy influence gene expression and life cycle characteristics in an invasive weed	[ <u>50</u> ]
Laboratory: spotted knapweed seeds and plants from throughout the North America and Europe	The population genetics of the fundamental cytotype- shift in invasive <i>Centaurea stoebe</i> s.l.: genetic diversity, genetic differentiation and small-scale genetic structure differ between cytotypes but not between ranges	[418]
Laboratory: spotted knapweed seeds from OR, ID, MT, France, Hungary, Romania, Switzerland	Plant invasions, generalist herbivores, and novel defense weapons	[423]
Laboratory: spotted knapweed seeds from an undescribed source	Influence of nutrient availability on the interaction between spotted knapweed and bluebunch wheatgrass	[200]
Models		
North America, Europe, and eastern Asia	Contrasting spatio-temporal climatic niche dynamics during the eastern and western invasions of spotted knapweed in North America	[ <u>44]</u>
North America, Europe, and eastern Asia	Evidence of climatic niche shift during biological invasion	[ <u>46</u> ]

Study location; plant community	Title	Control methods investigated	Reference
Forests			
BC: Wapiti Lake near Jaffray, Rabbit Ridge near Elko, and in the Pend d'Oreille valley; open, mixed-conifer forest with a bunchgrass understory and spotted knapweed	Interspecific interactions between the gall-fly <i>Urophora affinis</i> Frfld. (Diptera: Tephritidae) and the weevil <i>Larinus minut</i> us Gyll. (Coleoptera: Curculionidae), two biological control agents released against spotted knapweed, <i>Centaurea stobe</i> L. ssp. <i>micranthos</i>	Biocontrol ( <i>Larinus</i> minutus and <i>Urophora</i> <i>affinis</i> )	[100]
Steppe and sagebrush-steppe	•	•	
ID: Dubois; spotted knapweed- dominated sagebrush steppe rangeland	Developing prescription grazing guidelines for controlling spotted knapweed with sheep	Domestic sheep grazing	[ <u>174</u> ]
MT: Corvallis and Missoula; spotted knapweed stands in the field and in a common garden	Influence of seed head-attacking biological control agents on spotted knapweed reproductive potential in western Montana over a 30-year period	Mowing and biocontrol (Larinus spp., Metzneria paucipunctella, Urophora affinis, and Urophora quadrifasciata)	[471]
MT: Corvallis and Stevensville; fields with spotted knapweed	Decline of spotted knapweed density at two sites in western Montana with large populations of the introduced root weevil, <i>Cyphocleonus achates</i> (Fahraeus)	Biocontrol ( <i>Cyphocleonus achates</i> )	[ <u>461]</u>
MT: Glacier National Park; meadow dominated by spotted knapweed (40%–60% cover) and shortgrass prairie of the rough fescue and Idaho fescue community types	Restoration of spotted knapweed infested grasslands in Glacier National Park	Tilling, herbicide application (clopyralid), seeding of native graminoids and forbs, and planting of grass and forb seedlings	[474]
MT: Lolo National Forest; bluebunch wheatgrass-arrowleaf balsamroot communities with scattered ponderosa pine and Rocky Mountain Douglas-fir	Effects of picloram application on community dominants vary with initial levels of spotted knapweed ( <i>Centaurea stoebe</i> ) invasion	Herbicide application (picloram)	[ <u>358</u> ]
MT: Lolo National Forest; bluebunch wheatgrass-arrowleaf balsamroot communities with scattered ponderosa pine and Rocky Mountain Douglas-fir	Long-term effects of weed control with picloram along a gradient of spotted knapweed invasion	Herbicide application (picloram)	[ <u>354]</u>

Table A9—Publications from 1999 to 2021 about spotted knapweed's response to nonfire control methods.

MT: Lolo National Forest; grassland dominated by bluebunch wheatgrass, rough fescue, and Idaho fescue	Influence of spotted knapweed ( <i>Centaurea maculosa</i> ) management treatments on arbuscular mycorrhizae and soil aggregation	Herbicide application (picloram or clopyralid + 2,4-D), mowing, and hand pulling	[ <u>279</u> ]
MT: Lolo National Forest; spotted knapweed stands	Effect of root feeding insects on spotted knapweed ( <i>Centaurea</i> <i>maculosa</i> ) stand density	Biocontrol (Agapeta zoegana, Cyphocleonus achates, and Urophora affinis)	[ <u>86</u> ]
MT: Miles City; grasslands dominated by western wheatgrass	Assessing invasiveness of exotic weeds outside their current invasive range	Grazing by domestic sheep and cattle	[407]
MT: Missoula; a spotted knapweed and Idaho fescue dominated site	Shoot herbivory on the invasive plant, <i>Centaurea maculosa</i> , does not reduce its competitive effects on conspecifics and natives	Clipping and herbivory by a native moth ( <i>Trichoplusia ni</i> )	[ <u>341]</u>
MT: Missoula; rough fescue- bluebunch wheatgrass prairie with dense spotted knapweed	Non-target effects of broadleaf herbicide on a native perennial forb: A demographic framework for assessing and minimizing impacts	Herbicide application (picloram)	[ <u>98</u> ]
MT: Missoula; rough fescue/bluebunch wheatgrass and Idaho fescue/bluebunch wheatgrass grasslands with "light to moderate" spotted knapweed cover	Exotic weed control treatments for conservation of fescue grassland in Montana	Herbicide application (picloram, clopyralid, and 2,4-D)	[401]
MT: Missoula County; bluebunch wheatgrass and crested wheatgrass rangelands	Spotted knapweed management with integrated methods	Hand pulling and mowing, herbicide application (picloram and clopyralid + 2,4-D), and biocontrol ( <i>Cyphocleonus</i> <i>achates</i> )	[ <u>48]</u>
MT: Missoula County; Idaho fescue-bluebunch wheatgrass habitat type dominated by spotted knapweed	Soil nutrient availability as a mechanistic assessment of carbon addition and biological control of spotted knapweed (Centaurea maculosa Lam.)	Biocontrol ( <i>Cyphocleonus</i> achates) and ammonium nitrate and sucrose addition	[42]
MT: near Belgrade and Bozeman; Idaho fescue-bluebunch wheatgrass habitat types dominated in part by spotted knapweed	Spotted knapweed response to season and frequency of mowing	Mowing	[ <u>408]</u>
MT: near Bozeman; Idaho fescue- bluebunch wheatgrass habitat type dominated by spotted knapweed	Effects of the interaction of the biocontrol agent <i>Agapeta zoegana</i> L. (Lepidoptera: Cochylidae) and grass competition on spotted knapweed	Biocontrol (Agapeta zoegana)	[ <u>463]</u>

MT: near Bozeman; Idaho fescue-	Picloram, fertilizer, and defoliation	Herbicide application	[ <u>221</u> ]
bluebunch wheatgrass habitat	interactions on spotted knapweed	(picloram), nitrogen and	
type dominated by spotted	reinvasion	phosphorus addition, and	
knapweed		clipping grasses	
MT: near Bozeman; undescribed	Mowing: An important part of	Mowing	[433]
	integrated weed management		
MT: near Bozeman and Hamilton;	Enhancing intermediate wheatgrass	Tilling, herbicide	[442]
rough fescue-bluebunch	establishment in spotted knapweed	application (glyphosate),	
wheatgrass and Idaho fescue-	infested rangeland	and seeding of	
bluebunch wheatgrass habitat		intermediate wheatgrass	
types dominated by spotted			
knapweed			
MT: near Bozeman and Hamilton;	Integrating disturbance and	Tilling, herbicide	[ <u>441</u> ]
rough fescue-bluebunch	colonization during rehabilitation of	application (glyphosate),	
wheatgrass and Idaho fescue-	invasive weed-dominated grasslands	and seeding of	
bluebunch wheatgrass habitat		intermediate wheatgrass	
types dominated by spotted			
knapweed			
MT: near Bozeman and Missoula;	Spotted knapweed, forb, and grass	Herbicide application	[220]
a rough fescue-bluebunch	response to 2,4-D and N-fertilizer	(2,4-D) and nitrogen and	··
wheatgrass habitat type		phosphorus addition	
dominated by spotted knapweed			
and an Idaho fescue-bluebunch			
wheatgrass habitat type site with			
scattered spotted knapweed			
MT: near Bozeman and Norris;	Predicting plant community response	Herbicide application	[238]
Idaho fescue-bluebunch	to picloram	(picloram)	
wheatgrass type with patches of		, , , , , , , , , , , , , , , , , , ,	
spotted knapweed			
MT: near Drummond and	Integrating 2,4-D and sheep grazing	Herbicide application	[440]
Missoula; abandoned hayfields	to manage spotted knapweed	(2,4-D) and domestic	·
with Kentucky bluegrass,	infested rangeland	sheep grazing	
intermediate wheatgrass, and/or			
cheatgrass dominated by spotted			
knapweed			
MT: near Greenough; mountain	Sequential cattle and sheep grazing	Grazing by domestic	[195]
big sagebrush/rough fescue with	for spotted knapweed control	sheep and cattle	
spotted knapweed			
MT: near Hamilton; rough fescue-	Use of picloram to enhance	Herbicide application	[223]
bluebunch wheatgrass habitat	establishment of <i>Cyphoclenonus</i>	(picloram) and biocontrol	()
type dominated by spotted	achates (Coleoptera: Curculionidae)	(Cyphocleonus achates)	
knapweed and cheatgrass			

MT: near Hamilton and Missoula;	Povogotating spattad knowledd	Horbicido application	[420]
-	Revegetating spotted knapweed infested rangeland in a single entry	Herbicide application	[ <u>439</u> ]
rough fescue-bluebunch	intested rangeland in a single entry	(2,4-D, clopyralid,	
wheatgrass habitat types dominated by spotted knapweed		glyphosate, and	
,		picloram) and seeding	
and/or cheatgrass		native and nonnative	
		perennial grasses	[400]
MT: near Hamilton and Ronan;	Long-term population dynamics of	Tilling, herbicide	[ <u>409</u> ]
rough fescue-bluebunch	seeded plants in invaded grasslands	application (glyphosate,	
wheatgrass habitat types		2,4-D and picloram), and	
dominated by spotted knapweed		seeding of intermediate	
and/or sulphur cinquefoil		wheatgrass and a mix of	
		native perennial grasses	
MT: near Helmville; rough fescue-	Defoliation timing effects on spotted	Clipping	[ <u>28</u> ]
bluebunch wheatgrass habitat	knapweed seed production and		
type "moderately" invaded by	viability		
spotted knapweed			
MT: near Helmville; rough fescue-	Percent spotted knapweed	Grazing by domestic	[ <u>484]</u>
bluebunch wheatgrass habitat	(Centaurea stoebe) in the diets of	sheep	
type "moderately" invaded by	grazing sheep		
spotted knapweed			
MT: near Helmville; rough fescue-	Prescribed sheep grazing to suppress	Grazing by domestic	[ <u>499</u> ]
bluebunch wheatgrass habitat	spotted knapweed on foothill	sheep	
type, one with a "light infestation"	rangeland		
and another with a "moderate			
infestation" of spotted knapweed			
MT: near Missoula; spotted	Integrating herbicides and re-seeding	Herbicide application	[294]
knapweed and cheatgrass	to restore rangeland infested by an	(clopyralid, glyphosate,	
dominated communities	invasive forb-annual grass complex	picloram, imazapic, and	
		aminopyralid) and	
		seeding native and	
		nonnative perennial	
		grasses	
MT: near Polson; bluebunch	Combined herbivory by targeted	Biocontrol (Agapeta	[327]
wheatgrass/Sandberg bluegrass	sheep grazing and biological control	zoegana, Cyphocleonus	[ <u>327</u> ]
habitat type dominated by	insects to suppress spotted	achates, Larinus minutus,	
spotted knapweed	knapweed ( <i>Centaurea stoebe</i> )	and Larinus obtusus) and	
		grazing by domestic	
		<b>v v</b> ,	
MT: noor Donon: Idoho	Detential for successional theory to	sheep	
MT: near Ronan; Idaho	Potential for successional theory to	Herbicide application	[445]
fescue/bluebunch wheatgrass	guide restoration of invasive-plant-	(picloram and 2,4-D) and	
type dominated by nonnative	dominated rangeland	seeding common wheat	
annual and perennial grasses			

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MT: near Ronan; rough fescue- bluebunch wheatgrass vegetation	Augmentative restoration: Repairing damaged ecological processes during	Tilling, herbicide application (2,4-D),	[ <u>443</u> ]
type dominated by spotted	restoration of heterogeneous	watering, and seeding	
knapweed and sulphur cinquefoil	environments	native grasses and forbs	
MT: near Ronan; rough fescue-	Using ecological theory to guide the	Tilling, herbicide	[22]
bluebunch wheatgrass type	implementation of augmentative	application (2,4-D), and	
dominated by spotted knapweed	restoration	seeding native grasses	
and sulphur cinquefoil		and forbs	
MT: Pondera, Fergus, and	Field cage assessment of interference	Biocontrol (Bangasternus	[451]
Chouteau counties; dense spotted	among insects attacking seed heads	fausti, Larinus minutus,	
knapweed populations	of spotted and diffuse knapweed	and Urophora affinis)	
MT: Powell County; pasture in	Effects of training on cattle grazing	Grazing by cattle	[501]
sagebrush steppe with 35%	spotted knapweed and Canada thistle	Shulling by cuttle	[]
spotted knapweed and 55%			
crested wheatgrass cover			
MT: throughout southwestern	Ecological tradeoffs in non-native	Hand pulling and digging	[450]
MT; big sagebrush-grassland	plant management	and herbicide application	<u></u> ,
habitat type dominated by		(picloram)	
bluebunch wheatgrass, western		( /	
wheatgrass, and Idaho fescue			
AB: Waterton Lake National Park;	Spotted knapweed plant	Herbicide application	[232]
rough fescue grasslands	management and restoration of	(aminopyralid), hand	
	native grassland in Waterton Lakes	pulling, digging, and	
	National Park, Alberta	bagging	
AB: Waterton Lakes National Park;	Experimental control of spotted	Herbicide application	[346]
meadows with spotted knapweed	knapweed (Centaurea stoebe) within	(aminopyralid) and hand	
	critical habitat of the endangered	pulling	
	half-moon hairstreak butterfly		
	(Satyrium semiluna): A pilot study of		
	Blakiston Fan, Waterton Lakes		
	National Park, Alberta		
BC: southeastern BC; meadows	Role of plant phenology in mediating	Biocontrol (Larinus	[ <u>40]</u>
dominated by spotted knapweed	interactions between two biological	minutus and Urophora	
	control agents for spotted knapweed	affinis)	
BC: Thompson, Salmon, Nicola,	Impact of biological control on two	Biocontrol (various, not	[ <u>152</u> ]
Okanagan, Kettle, and	knapweed species in British Columbia	specified)	
Kootenay river valleys; grasslands			
within the bunchgrass and dry			
phases of the ponderosa pine and			
interior Douglas-fir Biogeoclimatic			
Zones			

Sand dunes			
MI: Grand Sable Dunes of Pictured	Effects of management on native and	Herbicide application	[ <u>264</u> ]
Rocks National Lakeshore; sand	exotic plant communities in Pictured	(aminopyralid and	
dunes with spotted knapweed	Rocks National Lakeshore in the	clopyralid)	
	Upper Peninsula of Michigan		
MI: Grand Sable Dunes of Pictured	Long-term effects of herbicide	Herbicide application	[ <u>165</u> ]
Rocks National Lakeshore; sand	treatments on spotted knapweed	(aminopyralid and	
dunes with spotted knapweed	and non-target plants in the Grand	clopyralid)	
	Sable Dunes		
Riparian areas			
CO: simulation model of spotted	Biological control and precipitation	Biocontrol (Cyphocleonus	[ <u>288</u> ]
knapweed population dynamics	effects on spotted knapweed	achates, Larinus minutus,	
using data from Lefthand Canyon	(Centaurea stoebe): Empirical and	and Urophora spp.)	
and a common garden	modeling results		
CO: near Boulder; meadow,	Effects of plant competition, seed	Biocontrol (Larinus	[ <u>250</u> ]
riparian areas, and adjacent	predation, and nutrient limitation on	minutus)	
ponderosa pine woodlands with	seedling survivorship of spotted		
spotted knapweed	knapweed (Centaurea stoebe)		
CO: near Boulder; meadow,	Factors affecting spotted knapweed	Biocontrol (Larinus	[ <u>289</u> ]
riparian areas, and adjacent	(Centaurea stoebe) seedling survival	minutus, Cyphocleonus	
ponderosa pine woodlands with	rates	achates, Sphenoptera	
spotted knapweed		<i>jugoslavica,</i> and	
		Urophora spp.)	
CO: near Boulder; meadow,	Interactions and effects of multiple	Biocontrol (Cyphocleonus	[ <u>427</u> ]
riparian areas, and adjacent	biological control insects on diffuse	achates, Larinus spp.,	
ponderosa pine woodlands with	and spotted knapweed in the Front	Sphenoptera jugoslavica,	
spotted knapweed	Range of Colorado	and Urophora species)	
CO: near Boulder; meadow,	Precipitation and the interaction of	Biocontrol (Larinus	[ <u>394</u> ]
riparian areas, and adjacent	seedhead biological control insects	minutus and Urophora	
ponderosa pine woodlands with	for spotted knapweed in the Rocky	affinis)	
spotted knapweed	Mountain Front Range		
CO: near Boulder; meadow,	Reconciling contradictory findings of	Biocontrol (Cyphocleonus	[248]
riparian areas, and adjacent	herbivore impacts on spotted	achates, Larinus minutus,	
ponderosa pine woodlands with	knapweed ( <i>Centaurea stoebe</i> ) growth	and Urophora spp.)	
spotted knapweed	and reproduction		
CO: near Boulder; meadow,	The lesser of two weevils:	Biocontrol (Cyphocleonus	[546]
riparian areas, and adjacent	physiological responses of spotted	achates and Larinus	
ponderosa pine woodlands with	knapweed ( <i>Centaurea stoebe</i> ) to	minutus)	
spotted knapweed	above- and belowground herbivory	,	
	by Larinus minutus and Cyphocleonus		
		1	1

			[001]
MI: along the Grand River; spotted	Native warm-season grass	Tilling, herbicide	[ <u>281</u> ]
knapweed-dominated sandy	establishment on spotted knapweed-	application (2,4-D and	
glacial outwash terrace	infested gravel mine spoils	glyphosate), sludge	
abandoned after being "heavily		application, and seeding	
disturbed" by gravel mining		native perennial grasses	
Roadsides and old fields			
AR: Washington County; roadsides	Seasonal dynamics and impact of	Biocontrol (Urophora	[ <u>108</u> ]
with spotted knapweed	Urophora quadrifasciata (Meigen)	quadrifasciata)	
	(Tephritidae: Diptera) on spotted		
	knapweed in the Arkansas Ozarks		
AR: Washington County; roadsides	Impact of roadside maintenance	Mowing and biocontrol	[ <u>139</u> ]
with spotted knapweed	practices on Larinus minutus	(Larinus minutus)	
	(Gyllenhal), a biological control agent		
	of spotted knapweed		
AR: Washington County; roadsides	Larinus minutus (Coleoptera:	Biocontrol (Larinus	[323]
with spotted knapweed	Curculionidae) and Urophora	minutus and Urophora	
	quadrifasciata (Diptera: Tephritidae),	quadrifasciata)	
	evidence for interaction and impact		
	on spotted knapweed in Arkansas		
AR: Washington and Benton	The biological control of spotted	Mowing and biocontrol	[324]
counties; a field dominated by	knapweed in the southeastern United	(Larinus minutus)	(
spotted knapweed and a field	States	(	
dominated by spotted knapweed,			
sumac, Johnsongrass, and			
purpletop			
Outside the US in Greece:	Notes on the biology of <i>Larinus</i>	Biocontrol ( <i>Larinus</i>	[235]
roadsides with spotted knapweed	minutus Gyllenhal (Col.,	minutus)	[233]
roadsides with spotted khapweed	Curculionidae), an agent for	mmatusj	
	biological control of diffuse and		
	spotted knapweeds		
Undescribed plant communities	spotted knapweeds		
CO: Fort Carson	Comparative fungal responses in	Seeding native and	[246]
	managed plant communities infested	nonnative perennial	[240]
		grasses and alfalfa,	
	by spotted ( <i>Centaurea maculosa</i>	•	
	Lam.) and diffuse ( <i>C. diffusa</i> Lam.)	sucrose addition, and	
	knapweed	whole soil incoculum	
ID: Lombi Country		application	[[]]
ID: Lemhi County	Goats: A tool for controlling spotted knapweed	Domestic goat grazing	[ <u>539]</u>
IN and MI: Elkhart County, IN, and	Establishment, impacts, and current	Biocontrol (Cyphocleonus	[72]
Crawford, Gogebic, Houghton,	range of spotted knapweed	achates and Larinus	
Ionia, Iron, Jackson, Kalamazoo,	(Centaurea stoebe ssp. micranthos)	minutus) and seeding	
Missaukee, Oakland, and	biological control insects in Michigan.	native perennial grasses	
Schoolcraft counties, MI		and forbs	

MI: Camp Ripley	Managing spotted knapweed	Herbicide application	[225]
	(Centaurea stoebe) using restoration	(aminopyralid), soil	
	methods	packing, and seeding	
		native perennial grasses	
MT	Evaluation of establishment of	Biocontrol (Agapeta	[477]
	Cyphocleonus achates and its	<i>zoegana</i> and	
	potential impact on spotted	Cyphocleonus achates)	
	knapweed		
MT	Spotted knapweed (Centaurea	Biocontrol (Larinus	[263]
	maculosa Lamarck) seed and	minutus, Urophora	
	Urophora spp. gall destruction by	affinis, and Urophora	
	Larinus minutus Gyllenhal	quadrifasciata)	
	(Coleoptera: Curculionidae)		
	combined with Urophora affinis		
	Frauenfeld (Diptera: Tephritidae) and		
	Urophora quadrifasciata (Meigen)		
	(Diptera: Tephritidae)		
TN: Cocke, Grainger, Greene, and	Assessment of insects, primarily	Biocontrol (Urophora	[252]
Hamblen counties	impacts of biological control	quadrifasciata)	·
	organisms and their parasitoids,	····	
	associated with spotted knapweed		
	( <i>Centaurea stoebe</i> L. s. l.) in eastern		
	Tennessee		
WA, ID, and MT	Managing noxious weeds on western	Herbicide application	[119]
	rangelands with aminopyralid	(aminopyralid)	
WA, OR, ID, WY and outside the	How do biological control and	Biocontrol (Larinus	[32]
US in Romania and Ukraine	hybridization affect enemy escape?	minimus)	
Outside the US in Russia	First report of a root and crown	Biocontrol (Rhizoctonia	[ <u>58</u> ]
	disease caused by Rhizoctonia solani	solani)	
	on Centaurea stoebe in Russia		
Animal enclosures, common garder	ns, greenhouses, and laboratories		
Animal enclosures: spotted	Seasonal change in nutrient	Grazing by domestic	[ <u>148</u> ]
knapweed plants from Dubois, ID	composition of spotted knapweed	sheep	
	and preference by sheep		
Animal enclosures: spotted	Conditioning ewes and lambs to	Grazing by domestic	[ <u>536</u> ]
knapweed plants from near	increase consumption of spotted	sheep	
Bozeman, MT	knapweed		
Animal enclosures: spotted	Will molasses or conditioning	Grazing by domestic	[ <u>535</u> ]
knapweed plants from near	increase consumption of spotted	sheep	
Bozeman, MT	knapweed by sheep?		
Animal enclosures and pastures:	Providing supplement, with or	Grazing by domestic	[ <u>78</u> ]
spotted knapweed plants from	without PEG, to reduce the effects of	sheep and cattle	
MT; pastures near Bozeman and	cnicin and enhance grazing on		
Deerlodge	spotted knapweed by sheep and		
	cattle		

Common garden: spotted	Compatibility of two herbicides with	Herbicide application	[ <u>464</u> ]
knapweed plants from near	Cyphocleonus achates (Coleoptera:	(2,4-D and clopyralid)	
Corvallis, MT	Curculionidae) and Agapeta zoegana	and biocontrol (Agapeta	
	(Lepidoptera: Tortricidae), two root	<i>zoegana</i> and	
	insects introduced for biological	Cyphocleonus achates)	
	control of spotted knapweed		
Common garden: spotted	Compatibility of seed head biological	Mowing and biocontrol	[ <u>469</u> ]
knapweed plants from an	control agents and mowing for	(Larinus spp., Metzneria	
undescribed source	management of spotted knapweed	paucipunctella, Urophora	
		affinis, and Urophora	
		quadrifasciata)	
Common garden: spotted	Effect of summer drought relief on	Biocontrol (Cyphocleonus	[ <u>94</u> ]
knapweed plants from an	the impact of the root weevil	achates)	
undescribed source	Cyphocleonus achates on spotted		
	knapweed		
Common garden: spotted	Impacts of the biological control	Biocontrol (Cyphocleonus	[ <u>93</u> ]
knapweed plants from an	agent Cyphocleonus achates on	achates)	
undescribed source	spotted knapweed, Centaurea		
	maculosa, in experimental plots		
Common garden: spotted	Root herbivores, pathogenic fungi,	Biocontrol (Agapeta	<u>[404]</u>
knapweed plants from an	and competition between Centaurea	zaegana and Sclerotinia	
undescribed source	maculosa and Festuca idahoensis	sclerotiorum)	
Common garden: spotted	Creating weed-resistant plant	Tilling and seeding	[ <u>429</u> ]
knapweed seeds from Deer Lodge,	communities using niche-	crested wheatgrass,	
MT	differentiated nonnative species	intermediate wheatgrass,	
		and alfalfa	
Common garden: spotted	Revegetating weed-infested	Tilling and seeding	[70]
knapweed seeds from Deer Lodge,	rangeland with niche-differentiated	crested wheatgrass,	
MT	desirable species	intermediate wheatgrass,	
		and alfalfa	
Common garden: spotted	Population-level compensation	Biocontrol (Cyphocleonus	[ <u>360]</u>
knapweed seeds from near	impedes biological control of an	achates)	
Missoula, MT	invasive forb and indirect release of a		
	native grass		
Common garden: spotted	The tortoise and the hare: Reducing	Biocontrol (Cyphocleonus	[376]
knapweed seeds from near	resource availability shifts	achates)	
Missoula, MT	competitive balance between plant	,	
· · · · · · · · · · · · · · · · · · ·	species		
Common garden: spotted	Additive effects of aboveground and	Biocontrol (Cyphocleonus	[251]
knapweed seeds from an	belowground herbivores on the	achates and Larinus	<b>·</b>
	C C		
undescribed source	dominance of spotted knapweed	<i>minutus</i> ) and ammonium	
undescribed source	dominance of spotted knapweed (Centaurea stoebe)	<i>minutus</i> ) and ammonium nitrate and sucrose	

Common garden, greenhouse, and laboratory: spotted knapweed	Influence of plant phenostage and ploidy level on oviposition and	Biocontrol ( <i>Agapeta zoegana</i> and	[ <u>89</u> ]
roots from Stevensville and Missoula, MT; seeds from various locations; caged field experiments conducted in Switzerland	feeding of two specialist herbivores of spotted knapweed, <i>Centaurea</i> <i>stoebe</i>	Cyphocleonus achates)	
Greenhouse: spotted knapweed	First report: spotted knapweed	Herbcide application	[291]
seeds from Mount Broadwood in the East Kootenays and near Vernon, BC	( <i>Centaurea stoebe</i> ) resistance to auxinic herbicides	(clopyralid, 2,4-D, picloram, and aminopyralid)	
Greenhouse: spotted knapweed	Defoliation effects on arbuscular	Inoculation with	[523]
seeds from an undescribed source and soils from Norris, MT	mycorrhizae and plant growth of two native bunchgrasses and an invasive forb	arbuscular mycorrhizae and clipping	
Greenhouse: spotted knapweed seeds from an undescribed source and soils from Norris, MT	Belowground mechanisms that affect nutrient uptake and response to herbivory of <i>Centaurea maculosa</i> and native bunchgrasses	Inoculation with arbuscular mycorrhizae, addition of nitrogen and phosphorus, and clipping	[ <u>556]</u>
Greenhouse: spotted knapweed seeds and soil from Missoula County, MT	Soil nutrient availability as a mechanistic assessment of carbon addition and biological control of spotted knapweed ( <i>Centaurea</i> <i>maculosa</i> Lam.)	Sucrose addition	[42]
Greenhouse and laboratory: spotted knapweed seeds from Latah County, ID	Multitrophic soil microbial community determinants of biological control of spotted knapweed ( <i>Centaurea stoebe</i> subsp. micranthos) by <i>Sclerotinia</i> <i>sclerotiorum</i>	Biocontrol (Sclerotinia sclerotiorum)	[106]
Greenhouse and laboratory: spotted knapweed seeds from Polo, IL	Altered gene expression in three plant species in response to treatment with Nep1, a fungal protein that causes necrosis	Nep1 application	[237]
Greenhouse and laboratory: spotted knapweed seeds from Polo, IL and Sidney, MT	Factors influencing the herbicidal activity of Nep1, a fungal protein that induces the hypersensitive response in <i>Centaurea maculosa</i>	Nep1 application and herbicide application (2, 4-D and glyphosate)	[ <u>17</u> ]
Laboratory: spotted knapweed plants from Russia, Hungary, and Slovak Republic	Identification, pathogenicity and comparative virulence of <i>Fusarium</i> spp. associated with insect-damaged, diseased <i>Centaurea</i> spp. in Europe	Biocontrol (Fusarium spp., Cyphocleonus spp., and Agapeta spp.)	[57]
Laboratory: spotted knapweed seeds from an undescribed source	Enhancing native forb establishment and persistence using a rich seed mixture	Seeding native annual and perennial forbs	[434]

Laboratory: spotted knapweed	Wheat gluten meal inhibits	Herbicide application	[ <u>162</u> ]
seeds from an undescribed source	germination and growth of broadleaf	(wheat gluten meal)	
	and grassy weeds		

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