13 Spotted Knapweed

J. Story

Montana State University, Western Agricultural Research Center,
Corvallis, Montana, USA

PEST STATUS OF WEED

Spotted knapweed, *Centaurea maculosa* Lamarck, is a purple-flowered, herbaceous, perennial weed, living three to five years on average. It infests semiarid range lands in the western United States and roadsides and fields in the eastern part of the country. Infested areas are dominated by the plant, reducing their grazing value and suppressing native plant communities. The plant, originally from Central Asia, has been in North America for over 120 years.

Nature of Damage

Economic damage. Spotted knapweed is a serious problem on rangeland, especially in the western United States. Bucher (1984) estimated that an 800,000 ha infestation in Montana was causing $4.5 million in annual forage losses, and that invasion of 13.6 million ha of vulnerable rangeland in Montana would cost cattle and sheep ranchers $155.7 million of gross revenue annually. Hirsh and Leitch (1996) reported that an 800,000 ha infestation of spotted knapweed, in combination with two knapweeds of minor importance in Montana (diffuse knapweed, *Centaurea diffusa* Lamarck, and Russian knapweed, *Acroptilon repens* [L] de Candolle) was causing $14 million in direct negative impacts and $28 million in indirect effects (i.e., reduced regional economy) to the state of Montana. Harris and Cranston (1979) reported that the 30,000 ha infestation in Canada was reducing forage production more than 88%. In the northeastern and northcentral United States, the plant is primarily a problem of roadsides, fields, and waste areas (Hoebeke, 1993); economic impact of the plant in those regions has not been reported.

Ecological damage. Spotted knapweed reduces livestock and wildlife forage (Thompson, 1996; Watson and Renney, 1974), increases surface water runoff and soil sedimentation (Lacey *et al.*, 1989), and lowers plant diversity (Tyser and Key, 1988). Spotted knapweed produces an allelopathic compound that reduces germination of some grass species (Kelsey and Locken, 1987).

Geographical Distribution

Spotted knapweed is native to Europe and western Asia but has become widespread in parts of the United States and Canada. The plant occurs throughout the United States except for Alaska, Texas, Oklahoma, Mississippi, and Georgia (USDA, NRCS, 2001). The plant is a serious invader of rangeland in the Rocky Mountain region. In Montana alone, the plant infests an estimated 1.9 million ha of rangeland and pasture (Lacey, 1989). In Canada, the plant is abundant in British Columbia, and is common in Ontario, Quebec, and the Maritimes (Watson and Renney, 1974).

BACKGROUND INFORMATION ON PEST PLANT

Taxonomy

The taxonomy of *C. maculosa* has been detailed by Dostal (1976) and reviewed by Müller *et al.* (1988) and Müller (1989). *Centaurea maculosa* is comprised of several subspecies occurring from western Asia to western Europe. The *C. maculosa* occurring in North America is a short-lived perennial tetraploid (2n=36) that is considered the same as *C. biebersteinii* de Candolle subsp. *biebersteinii* (=*C. micranthos* Gmelin ex. Hayek), a native of western Asia. However, the most widely distributed *C. maculosa* in Europe is the biennial diploid (2n=18) *C. maculosa* spp. *rhenana* (Boreau) Gugler (Dostal, 1976; Müller *et al.*, 1988; Müller, 1989).

Biology

Spotted knapweed is a purple-flowered, herbaceous weed, 30 to125 cm tall, with one to 10 upright stems, and a stout taproot (Fig. 1). The plant is a perennial, living an average of three to five years and frequently up to nine years (Boggs and Story, 1987). The flower heads, enclosed by black-tipped bracts, are borne singly at the terminal ends of branches. Seed is shed immediately upon maturation of the seed head. The plant reproduces solely by seed. Seed production ranges from 5,000 to 40,000 seeds/m^2 (Sheley *et al.*, 1998). Seeds can survive in the soil for eight or more years (Davis *et al.*, 1993).

Figure 1. Spotted knapweed, *Centaurea maculosa* Lamarck. (Photo by Jim Story.)

The life history of the plant has been described by Watson and Renney (1974). Seed germination occurs in the fall or early spring, depending upon moisture availability. Seedlings develop into rosettes; plants that have overwintered as rosettes usually produce floral stems the following summer. Stem elongation occurs in June followed by flowering in July and seed dispersal in August.

Spotted knapweed is adapted to a range of habitats and soil types, but is especially well suited to relatively dry sites (Watson and Renney, 1974). In Europe, the plant is most aggressive in the forest steppe but can form dense stands in more moist areas on well-drained soils including gravel, and in drier sites where summer precipitation is supplemented by runoff (Sheley *et al.*, 1998).

Analysis of Related Native Plants in the Eastern United States

The North American plants most closely related to spotted knapweed include safflower (*Carthamus tinctorius* L.) and possibly the two "knapweeds," *Centaurea americana* and *Centaurea rothrockii.* Recent evaluations, however, suggest the latter two plants should be treated as *Plectocephalus americanus* (Nutt.) (Müller-Schärer and Schroeder, 1993). The next closest relatives of spotted knapweed are members of the tribe Cardueae, mainly Carduinae (*Cirsium* and *Cynara* [e.g., artichoke]). There are numerous *Cirsium* species native to North America.

HISTORY OF BIOLOGICAL CONTROL EFFORTS IN THE EASTERN UNITED STATES

Area of Origin of Weed

The native range of the spotted knapweed (tetraploid) occurring in North America is eastern Europe and western Asia (Müller *et al.*, 1989).

Areas Surveyed for Natural Enemies

Surveys were conducted throughout Europe and western Asia for natural enemies.

Natural Enemies Found

Schroeder (1985) listed 38 arthropod species that were known to be associated with spotted knapweed in Eurasia. Of these, 12 species were screened and released in North America against the plant (Table 1).

Host Range Tests and Results

The number of plants included in the test plant list for each of the 12 insect species varied, but averaged around 45 test plant species per insect. Most of the plant species used were from the family Asteraceae, but representative species from one or more other families also were often tested. Particular emphasis was placed on plants in the Asteraceae tribe Cardueae which includes the genus *Centaurea*. The test plant list for *Larinus minutus* is presented in Table 2 (Jordan, 1995) because it is fairly representative of the plants tested on all 12 insect species. The only plants of economic importance in North America included in the tests were *Carthamus tinctorius* L. (safflower),

Table 1. Insects Released in the United States for Biological Control of Spotted Knapweed

Scientific Name	Insect Type	Plant Part Attacked	Where Collected	Date of First U.S. Release	State/Date of Release in Eastern U.S. and Canada	Known Estab. in Eastern U.S. and Canada
Urophora affinis Frauenfeld	Fly (Tephritidae)	Flower head	France, Austria	1973	IN 1997 MD 1983 NY 1983 VA 1986 MN 1990 WI 1991 MI 1994 Quebec 1979 Ontario 1970	 x x x x x x
Urophora quadrifasciata (Meigen)	Fly (Tephritidae)	Flower head	Former USSR	1980	Quebec 1979 MD 1983 NY 1983 VA 1986 MN 1990 WI 1991 MI 1994 IN 1997	x x x x x x x
Terellia virens (Loew)	Fly (Tephritidae)	Flower head	Austria, Switzer.	1992	MN 1994	
Chaetorellia acrolophi White and Marquardt	Fly (Tephritidae)	Flower head	Austria,Switzer.	1992	MN 1996	
Metzneria paucipunctella Zeller	Moth (Gelechiidae)	Flower head	Switzer.	1980	MN 1991 VA 1986	 x
Agapeta zoegana L.	Moth (Cochylidae)	Root	Austria, Hungary	1984	IN 1996 MN 1991 WI 1991	 x
Pterolonche inspersa Staudinger	Moth (Pterolonchida-e)	Root	Hungary	1988	-	
Pelochrista medullana (Staudinger)	Moth (Tortricidae)	Root	Austria, Hungary	1984	-	
Cyphocleonus achates (Fahraeus)	Weevil (Curculionidae)	Root	Austria, Romania	1988	IN 1996 MN 1994	
Bangasternus fausti Reitter	Weevil (Curculionidae)	Flower head	Greece	1990	MN 1992	
Larinus obtusus Gyllenhal	Weevil (Curculionidae)	Flower head	Romania, Serbia	1992	MN 1995	
Larinus minutus Gyllenhal	Weevil (Curculionidae)	Flower head	Greece, Romania	1991	IN 1996 MN 1994	x x

Helianthus annuus L., (common sunflower), and *Cynara scolymus* L. (globe artichoke). None of the insects oviposited or fed on any of these three plants except for *Cyphocleonus achates* adults which fed slightly on artichoke. The feeding by *C. achates* was not of concern, however, because no eggs were laid on the plant. In general, attack by all of the insects was restricted to the genus *Centaurea*, and usually to

Table 2. Test plant list used for *Larinus minutus*

FAMILY: ASTERACEAE
- **Tribe: Cardueae**
  - Subtribe: Centaureinae
    - Genus: *Centaurea*
      - Subgenus: *Acrolophus*
        - *Centaurea arenaria* Bieb.
        - *C. cineraria* L.
        - *C. diffusa* Lamarck Europe
        - *C. diffusa* USA
        - *C. friderici* Vis.
        - *C. maculosa* Lamarck Europe
        - *C. maculosa* USA
        - *C. micranthos* S. G. Gmelin
        - *C. paniculata* L.
        - *C. vallesiaca* (D. C.) Jordan
      - Subgenus *Calcitrapa*
        - *C. calcitrapa* L.
        - *C. iberica* Trev. Sprengel
      - Subgenus: *Cartholepis*
        - *C. macrocephala* Muss.
      - Subgenus: *Centaurea*
        - *C. ruthenica* Lamarck
      - Subgenus: *Cyanus*
        - *C. cyanus* L.
        - *C. montana* L.
      - Subgenus: *Jacea*
        - *C. jacea* L.
        - *C. nigra* L.
        - *C. nigrescens* Willd.
        - *C. pannonica* (Heuffel) Simonkai
        - *C. phrygia*
      - Subgenus *Lopholoma*
        - *C. scabiosa* L.
      - Subgenus: *Phalolepis*
        - *C. alba* L.
      - Subgenus: *Psephellus*
        - *C. dealbata* Willd.
      - Subgenus: *Seridia*
        - *C. aspera* L.
        - *C. napifolia*
      - Subgenus: *Solstitiaria*
        - *C. nicaeensis* All.
        - *C. solstitialis* L.
    - other genera:
      - *Acroptilon repens* (L.) D. C.
      - *Carduncellus monspelliensum* All.
      - *Carthamus tinctorius* L.
      - *Cnicus benedictus* L.
      - *Crupina vulgaris* Pers.
      - *Mantisalca salmantica* Brig. and Cavillier
      - *Plectocephalus americanus* (Nutt.)
  - Subtribe: Carduinae
    - *Arctium lappa* L.
    - *Carduus acanthoides* L.
    - *C. nutans* L.
    - *Cirsium arvense* (L.) Scop.
    - *C. crassicaule* (Greene) Jeps.
    - C. creticum
    - *C. undulatum* (Nutt.) Spreng.
    - *Cynara scolymus* L.
    - *Galactites tomentosa*
    - *Onopordum acanthium* L.
    - *Silybum marianum* (L.) Gaertn.
  - **Tribe: Anthemideae**
    - *Achillea millefolium* L.
    - *Anthemis tinctoris* L.
    - *Artemisia absinthium* L.
    - *Chrysanthemum leucanthemum* L.
  - **Tribe: Astereae**
    - *Aster novi-belgii* L.
    - *Solidago canadensis* L.
  - **Tribe: Calenduleae**
    - *Calendula officinalis* L.
  - **Tribe: Carlineae**
    - *Carlina vulgaris* L.
  - **Tribe: Cichorieae**
    - *Cichorium intybus* L.
    - *Taraxacum officinale* Web.
  - **Tribe Echinopeae**
    - *Echinops sphaerocephalus* L.
  - **Tribe Heliantheae**
    - *Helianthus annuus* L.
    - *H. decapetatus* L.
    - *H. tuberosus* L.
    - *Rudbeckia hirta* L.
  - **Tribe: Inuleae**
    - *Inula helenium*
    - *Helichrysum orientale* (L.) Gaertn.
  - **Tribe: Senecioneae**
    - *Senecio jacobaea* L.

FAMILY: CARYOPHYLLACEAE
- *Dianthus superbus*
- *Silene vulgaris* (Moench) Garcke

FAMILY: CHENOPODIACEAE
- *Beta vulgaris* L.

FAMILY: CISTACEAE
- *Helianthemum vulgare* Gaertn.

FAMILY: CRUCIFERAE
- *Brassica oleracea* L.

FAMILY: DIPSACACEAE
- *Dipsacus fullonum* L.

FAMILY: POLYGONACEAE
- *Rumex acetosa* L.

FAMILY: RANUNCULACEAE
- *Delphinium elatum* L.

FAMILY: UMBELLIFERAE
- *Apium graveolens* L.
- *Daucus carota* L.

the subgenus *Acrolophus*. There has been no report of attack on non-target species by any of the insects since release, although specific surveys have apparently not been conducted.

Releases Made

Of the 12 biological control agent species released against spotted knapweed in the United States, 10 species have been released against spotted knapweed in the eastern United States and five (Table 1) have become established (Hoebeke, 1993; Wheeler, 1995; Mays and Kok, 1996; Wheeler and Stoops, 1996; Lang *et al.*, 1997; Lang, pers. comm.). The root moth, *Pelochrista medullana* (Staudinger) (Lepidoptera: Tortricidae) and the root moth, *Pterolonche inspersa* Staudinger (Lepidoptera: Pterolonchidae) were not released in the eastern United States due to insufficient numbers.

BIOLOGY AND ECOLOGY OF KEY NATURAL ENEMIES

Urophora affinis Frauenfeld (Diptera: Tephritidae)

Urophora affinis is a small (4.5 mm) fly that attacks the flower heads of spotted knapweed (Fig. 2). The fly is distinguished from other knapweed tephritids by the bright yellow spot on its black thorax, the black abdomen, and the light-colored markings on its wings. Collected in France and Austria, the first United States release was made in Montana and Oregon in 1973 (Maddox, 1982).

Larval feeding causes the formation of hard, woody galls in the receptacle tissue. The galls divert plant nutrients, resulting in reduced seed production in both attacked and unattacked seed heads on a plant. *Urophora affinis* is currently reducing seed production of spotted knapweed in the Pacific Northwest close to the threshold needed to achieve economic control (Harris and Shorthouse, 1996).

Fly larvae overwinter within galls (one larva per gall) and pupate in May, followed by adult emergence in late June and July. *Urophora affinis* is generally univoltine although a small percentage (approximately 7%) emerge in August and complete a second generation (Zwölfer, 1970; Gillespie, 1983; Story *et al*., 1992).

Urophora quadrifasciata (Meigen) (Diptera: Tephritidae)

Urophora quadrifasciata is a small (4.5 mm) fly that attacks the flower heads of spotted knapweed (Fig. 3). The fly is distinguished from other knapweed tephritids by its relatively dark body and the dark bands in the shape of the letters "UV" on its wings. The general biology of *U. quadrifasciata* is similar to that of *U. affinis* except that *U. quadrifasciata* forms papery galls in the ovary, attacks larger flower heads than does *U. affinis*, and is generally bivoltine (Harris, 1980; Gillespie, 1983).

Urophora quadrifasciata was introduced into British Columbia in 1972 (Harris, 1980), but not into the United States. However, by the early 1980s, the fly had dispersed into the Pacific Northwest states. *Urophora quadrifasciata* is now more widely distrib-

Figure 2. *Urophora affinis* Frauenfeld. (Photo by Robert Richard. USDA, APHIS, PPQ.)

Figure 3. *Urophora quadrifasciata* (Meigen). (Photo by Robert Richard, USDA, APHIS, PPQ.)

uted than *U. affinis*. *Urophora quadrifasciata* is common in many areas of the northeast and is very abundant in some areas of upstate New York (Blossey, unpub.data). However, *U. quadrifasciata* numbers remain low in areas where the two *Urophora* spp. coexist.

Metzneria paucipunctella Zeller (Lepidoptera: Gelechiidae)

Metzneria paucipunctella is a small (9 mm), univoltine moth that attacks the flower heads of spotted knapweed (Fig. 4). The moth is tan with small black spots. Originally collected in Switzerland, the moth was introduced into British Columbia in 1973 (Harris and Myers, 1984). Moths collected from British Columbia were subsequently introduced into the United States in Montana in 1980 (Story *et al.*, 1991a).

Figure 4. *Metzneria paucipunctella* Zeller. (Photo by Robert Richard, USDA, APHIS, PPQ.)

Metzneria paucipunctella overwinters as larvae in seed heads. Pupation occurs in May, followed by adult emergence in June and early July. Young larvae feed on developing seeds while older larvae feed on mature seeds and mine the receptacle. Older larvae bind several seeds together with silk webbing, which prevents dispersal of those seeds at maturity. Due to strong intraspecific competition, only one larva survives per seed head (Englert, 1971). Each larva destroys an average of eight seeds per seed head (Story *et al.*, 1991a). Larvae also will attack and destroy other seed head insects, including larvae of the two established seed head flies, *Urophora* spp. (Story *et al.*, 1991a). *Metzneria paucipunctella* frequently suffers high overwintering mortality.

Agapeta zoegana L. (Lepidoptera: Cochylidae)

Agapeta zoegana is a small (9 mm), yellow and brown, univoltine moth that attacks the roots of spotted knapweed (Müller *et al.*, 1988) (Fig. 5). Collected in Austria and Hungary, the first United States release of the moth was made in Montana in 1984 (Story *et al.*, 1991b).

Figure 5. *Agapeta zoegana* L. (Photo by Jim Story.)

Agapeta zoegana overwinters as larvae in roots. Adult emergence occurs from mid-June to early September. Females begin mating the first night after emergence and begin laying eggs the following evening. Adults live for nine to 11 days and each female lays an average of 75 eggs (up to 290), mostly within a four-day period. Larvae hatch in seven to 10 days and begin mining in the epidermal tissues of the root crown. Older larvae mine in the cortex and endodermis tissues and several larvae may develop in the same root. *Agapeta zoegana* has one generation per year. Studies in Montana indicate the moth is reducing the biomass of knapweed at some sites (Story *et al.*, 2000). Analyses by Clark *et al.* (2001a) suggest that probability of *A. zoegana* establishment at release sites is affected by soil type and the shape (patchy, continuous or linear) of the weed infestation.

Cyphocleonus achates (Fahraeus) (Coleoptera: Curculionidae)

Cyphocleonus achates is a large (19 mm), gray and black mottled weevil that attacks the roots of spotted knapweed (Fig. 6). Collected in Austria and Romania, the first United States release of the weevil was made in Montana in 1988 (Story *et al.*, 1997).

Figure 6. *Cyphocleonus achates* (Fahraeus). (Photo by CABI Bioscience.)

This univoltine weevil overwinters as larvae in roots. Adults emerge from mid-July to October and live eight to 15 weeks. Each female lays from one to three eggs per day throughout her adult life. Larvae hatch in 10 to 12 days and mine into the root cortex, eventually causing the formation of a conspicuous root gall. Dispersal is slow as adults don't fly (Stinson *et al.*, 1994).

Studies by Clark *et al.* (2001a) suggest that probability of *C. achates* establishment at release sites is affected by elevation, the shape (patchy, continuous or linear) of the weed infestation, and the number of years in which releases are made.

Larinus minutus Gyllenhal (Coleoptera: Curculionidae)

Larinus minutus is a small (4.5 mm) univoltine weevil that attacks flower heads of diffuse and spotted knapweed (Jordan, 1995) (Fig. 7). Collected in Greece and Romania, the weevil was introduced into the United States in Montana, Washington, and Wyoming in 1991 (Lang *et al.*, 1996).

Figure 7. *Larinus minutus* Gyllenhal. (Photo by Robert Richard, USDA, APHIS, PPQ.)

Weevils overwinter as adults in soil and become active in early June. Eggs are deposited into freshly opened flower heads during late July through early September. Larvae hatch in about three days and immediately feed downwards into the flower head, where they eat seeds and pappus hairs. Larval development is completed in about 28 days followed by a short pupation period (one to two weeks; Jordan, 1995). Adult *L. minutus* emerge from the seed head in late September and October and feed on knapweed leaves for a short period before entering the soil to overwinter.

Larinus minutus has developed large populations on diffuse knapweed in Washington, Montana, and Oregon, but population increase on spotted knapweed has been slow.

Larinus obtusus Gyllenhal (Coleoptera: Curculionidae)

Larinus obtusus is a small (5 mm) univoltine weevil that attacks the flower heads of spotted knapweed (Groppe, 1992). The weevil is slightly larger than *L. minutus*. Collected in Romania and Serbia, *L. obtusus* was introduced into the United States in Montana in 1992 (Story, unpub. data). The insect is established in moderate numbers in Montana.

Adult weevils become active in May and June and eggs are deposited into freshly opened flower heads in July. Larvae hatch in about four days and immediately feed downward into the flower head, where they eat seeds and pappus hairs. Larval development is completed in about 17 days followed by a nine-day pupation period. Adults of the new generation emerge from the seed head in late summer, approximately 30 days after egg deposition. Adults feed on knapweed leaves for a short period before entering the soil to overwinter.

Bangasternus fausti Reitter (Coleoptera: Curculionidae)

Bangasternus fausti is a small (4.5 mm) univoltine weevil that attacks the flower heads of spotted knapweed (Sobhian *et al.*, 1992). The weevil, collected in Greece, was introduced into the United States in 1990 (Rees *et al.*, 1995).

Adults become active in May and June and eggs are deposited (usually singly) on the stems or bracts of flower heads that are 3.0 to 3.5 mm in diameter. Females cover eggs with a black, hard material. Eggs hatch in eight to12 days and larvae tunnel through

the stem until they enter the flower head. Larvae from eggs laid on the flower head tunnel directly into the flower head. Once in the flower heads, larvae consume florets and ovules. Adults of the new generation emerge from the seed head in late summer and later enter the soil to overwinter. The period from egg to adult is about 32 days.

Chaetorellia acrolophi White and Marquardt (Diptera: Tephritidae)

Chaetorellia acrolophi is a small (4.5 mm) fly that attacks the flower heads of spotted knapweed (Fig. 8). The fly is distinguished from other knapweed tephritids by having nine black spots on a light-colored thorax, a light-colored abdomen, and light-colored markings on the wings in a "UV" pattern similar to that of *U. quadrifasciata*. *Chaetorellia acrolophi* was collected in Austria and Switzerland and introduced into the United States in Montana in 1992 (Story, unpub. data). Establishment rates have been very low in most states.

Figure 8. *Chaetorellia acrolophi* White and Marquardt. (Photo by CABI Bioscience.)

Chaetorellia acrolophi overwinters as larvae in seed heads. Pupation occurs in May, followed by adult emergence in June and early July. Eggs are deposited into unopened flower heads from June to July. Larvae hatch in about four days and immediately travel to the center of the flower head, where they burrow into florets. Older fly larvae attack several young seeds, additional florets, and parts of the seed head receptacle. The fly has two generations per year. Larvae and pupae of the first generation of *C. acrolophi* are white, while second generation larvae and pupae are yellow (Groppe and Marquardt, 1989a).

Terellia virens (Loew) (Diptera: Tephritidae)

Terellia virens is a small (4.5 mm) fly that attacks the flower heads of spotted knapweed (Fig. 9). The fly is distinguished from other knapweed tephritids by its lack of wing markings, its light-colored abdomen, and the faint spots on its light-colored thorax. *Terellia virens*, collected in Austria and Switzerland, was introduced into the United States in Montana in 1992 (Story, unpub. data). Establishment rates have been very low in most states.

Figure 9. *Terellia virens* (Loew). (Photo by CABI Bioscience.)

The fly overwinters as larvae in seed heads. Pupation occurs in May, followed by adult emergence in June and early July. Eggs are deposited into flower heads that are beginning to open. Larvae hatch in about four days and immediately burrow into young seeds (one larva per seed). Older larvae attack several young seeds and occasionally feed on the seed head receptacle. *Terellia virens* often has two generations, depending upon fall weather (Groppe and Marquardt, 1989b).

EVALUATION OF PROJECT OUTCOMES

Establishment and Spread of Agents

Of the natural enemy species released against spotted knapweed in the eastern United States and Canada, the following have been established: *Urophora affinis* (Virginia, New York, Pennsylvania, Minnesota, Wisconsin, Michigan, Quebec); *Urophora quadrifasciata* (Connecticut, Indiana, Maryland, Massachusetts, Michigan, Minnesota, New Hampshire, New Jersey, New York, Pennsylvania, Rhode Island, Vermont, West Virginia, Wisconsin, and Que-

bec); *Metzneria paucipunctella* (Virginia); *Agapeta zoegana* (Minnesota); and *Larinus minutus* (Indiana, Minnesota) (Hoebeke, 1993; Wheeler, 1995; Wheeler and Stoops, 1996; Mays and Kok, 1996; Lang *et al.*, 1997; Lang, pers. comm.) (Table 1). Except for the two *Urophora* species, particularly *U. quadrifasciata,* dispersal of the knapweed agents has been modest. An assessment of the *Urophora* spp. spread was conducted in Montana (Story *et al.*, 1987).

Suppression of Target Weed

Effects of imported natural enemies on spotted knapweed densities in the eastern United States have not been examined. However, impact information has been collected at sites in the western United States. Studies in Montana indicate that the two *Urophora* spp. are reducing spotted knapweed seed production by a minimum of 40% (Story *et al*., 1989), seed reduction by the *Urophora* spp. is further increased when *M. paucipunctella* is present (Story *et al.*, 1991a), and *A. zoegana* is significantly reducing the biomass of spotted knapweed at some sites (Story *et al.,* 2000). Spotted knapweed density is significantly reduced at two sites in western Montana where *C. achates* is well established (Story, unpub. data). Clark *et al.* (2001b) reported that spotted knapweed stem density, at 13 sites in Montana and adjacent states where *U. affinis* and one or both root feeding species of natural enemies (*A. zoegana, C. achates*) were established, declined from about 15 plants per m^2 in 1991 to1993 to seven plants in 1997 to 1998.

Effects on Native Plants

Neither the impact of these released agents on native, non-target plants, nor the recovery of native plant communities as weed densities, decline have been examined.

Economic Benefits

The economic benefits of biological control have not been realized yet, even in the west where some agents have been established for more than 15 years. However, given the reductions in knapweed density recently observed at localized infestations in Montana, economic benefits should be measurable in many states in the near future.

RECOMMENDATIONS FOR FUTURE WORK

Because of the large infestations of spotted knapweed in the west and the wide distribution in the north central and eastern United States, extensive redistribution of established biological control agents is required throughout much of the country. For preventative purposes, releases of the agents should be made in all states having only small populations of the weed.

The potential of most of the agents has not yet been realized in the west due to the large size of the infestations and the agents' modest rate of population increase. The control agents currently established in the United States are probably capable of reducing spotted knapweed densities in most locations.

There will undoubtedly be locations where the biological control agents are not effective. For example, early observations suggest the current complex of biological control agents in North America may not be effective on knapweed growing at higher elevations (>1,800 m). There are several niches on the plant (e.g., meristem, root collar, stems) that are not being exploited by the current agents in North America. If the need for further agents is deemed necessary, exploration for agents should be concentrated in Asia on tetraploid plants, with some emphasis on those agents attacking the currently unoccupied niches and those occurring at higher elevations.

Evaluation of the agents' impact is a priority goal now that some agent populations are reaching high levels at some locations in the west. Evaluation efforts may soon be possible at the smaller infestations in the east, especially in the northcentral states where the root insects, *A. zoegana* and *C. achates*, have been introduced.

REFERENCES

Boggs, K. W. and J. M. Story. 1987. The population age structure of spotted knapweed (*Centaurea maculosa*) in Montana. *Weed Science* 35:194-198.

Bucher, R. F. 1984. Potential spread and cost of spotted knapweed on range. *MontGuide* No. MT8423. Montana Cooperative Extension Service, Bozeman, Montana.

Clark, S. E., R. G. Van Driesche, N. Sturdevant, J. Elkinton, and J. P. Buonaccorsi. 2001a. Effects of site characteristics and release history on establishment of *Agapeta zoegana* (Lepidoptera: Cochylidae) and *Cyphocleonus achates* (Coleoptera: Curculionidae), root feeding herbivores attacking spotted knapweed, *Centaurea maculosa. Biological Control* 22: 122-130.

Clark, S. E., R. G. Van Driesche, and N. Sturdevant. 2001b. Effect of root feeding insects on spotted knapweed, *Centaurea maculosa*, stand density. *Southwestern Entomologist* 2: 129-135.

Davis, E. S., P. K. Fay, T. K. Chicoine, and C. A. Lacey. 1993. Persistence of spotted knapweed (*Centaurea maculosa*) seed in soil. *Weed Science* 41: 57-61.

Dostal, J. 1976. Centaurea L., pp. 254-301. *In* Anon. *Flora Europaea*, Vol. 4. Cambridge University Press, Cambridge, United Kingdom.

Englert, W. 1971. *Metzneria paucipunctella* Zel. (Gelechiidae, Lepidoptera): a potential insect for the biological control of *Centaurea stoebe* L. in Canada, pp. 161-165. *In* Dunn, P. (ed.). *Proceedings of the Second International Symposium on Biological Control of Weeds*, October 4-7. Rome, Italy.

Gillespie, R. L. 1983. Bionomics of *Urophora affinis* Frauenfeld, and *U. quadrifasciata* Meigen (Diptera: Tephritidae) in Northern Idaho. M. S. thesis, University of Idaho, Moscow, Idaho, USA.

Groppe, K. 1992. *Larinus obtusus Gyll. (Col: Curculionidae), a Candidate for Biological Control of Diffuse and Spotted Knapweed*. CAB International Institute of Biological Control Final Report, Silwood Park, Berks, United Kingdom.

Groppe, K. and K. Marquardt. 1989a. *Chaetorellia acrolophi White and Marquardt (Diptera: Tephritidae), a Suitable Candidate for the Biological Control of Diffuse and Spotted Knapweed in North America*. CAB International Institute of Biological Control Final Report, Silwood Park, Berks, United Kingdom.

Groppe, K. and K. Marquardt. 1989b. *Terellia virens (Loew) (Diptera: Tephritidae), a Suitable Candidate for the Biological Control of Diffuse and Spotted Knapweed in North America.* CAB International Institute of Biological Control Final Report, Silwood Park, Berks, United Kingdom.

Harris, P. 1980. Establishment of *Urophora affinis* Frfld. and *U. quadrifasciata* (Meig.) (Diptera: Tephritidae) in Canada for the biological control of diffuse and spotted knapweed. *Zeitschrift für angewandte Entomologie* 89: 504-514.

Harris, P. and R. Cranston. 1979. An economic evaluation of control methods for diffuse and spotted knapweed in western Canada. *Canadian Journal of Plant Science* 59: 375-382

Harris, P. and J. D. Shorthouse. 1996. Effectiveness of gall inducers in weed biological control. *The Canadian Entomologist* 128: 1021-1055.

Harris, P. and J. H. Myers. 1984. *Centaurea diffusa* Lam. and *C. maculosa* Lam. s. lat., diffuse and spotted knapweed (Compositae), pp. 127-137. *In* Kelleher, J. and M. Hulme (eds.). *Biological Control Programmes against Insects and Weeds in Canada 1969-1980*. Commonwealth Agricultural Bureau, Slough, United Kingdom.

Hirsch, S. A. and J. A. Leitch. 1996. The impact of knapweed on Montana's economy. Agricultural Economics Report No. 355. North Dakota Agricultural Experiment Station. Fargo, North Dakota, USA.

Hoebeke, E. R. 1993. Establishment of *Urophora quadrifasciata* (Diptera: Tephritidae) and *Chrysolina quadrigemina* (Coleoptera: Chysomelidae) in portions of eastern United States. *Entomological News* 10: 143-152.

Jordan, K. 1995. Host specificity of *Larinus minutus* Gyll. (Col., Curculionidae), and agent introduced for the biological control of diffuse and spotted knapweed in North America. *Journal Applied Entomology* 119: 689-693.

Kelsey, R. G. and L. J. Locken. 1987. Phytotoxic properties of cnicin, a sesqiterpene lactone from *Centaurea maculosa* (spotted knapweed). *Journal of Chemical Ecology* 13: 19-33.

Lacey, C. 1989. Knapweed management - a decade of change, pp. 1-6. *In* Anon*. Proceedings of the Knapweed Symposium*. Montana State University, Bozeman, Montana, USA.

Lacey, J. R., C. B. Marlow, and J. R. Lane. 1989. Influence of spotted knapweed (*Centaurea maculosa*) on surface runoff and sediment yield. *Weed Technology* 3: 627-631.

Lang, R. R., R. D. Richard, and R. W. Hansen. 1997. *Urophora affinis* and *U. quadrifasciata* (Diptera: Tephritidae) released and monitored by USDA, APHIS, PPQ as biological control agents of spotted and diffuse knapweed. *The Great Lakes Entomologist* 30: 105-113.

Lang, R. F., J. M. Story, and G. L. Piper. 1996. Establishment of *Larinus minutus* Gyllenhal (Coleoptera: Curculionidae) for biological control of diffuse and spotted knapweed in the western United States. *Pan Pacific Entomologist*. 72: 209-212.

Maddox, D. M. 1982. Biological control of diffuse knapweed (*Centaurea diffusa*) and spotted knapweed (*Centaurea maculosa*). *Weed Science* 30: 76-82.

Mays, W. T. and L.-T. Kok. 1996. Establishment and dispersal of *Urophora affinis* (Diptera: Tephritidae) and *Metzneria paucipunctella* (Lepidoptera: Gelechiidae) in southwestern Virginia. *Biological Control* 6: 299-305.

Müller, H. 1989. Growth pattern of diploid and tetraploid spotted knapweed, *Centaurea maculosa* Lam. (Compositae), and effects of the root-mining moth *Agapeta zoegana* (L.) (Lep.: Cochylidae). *Weed Research* 29: 103-111.

Müller-Schärer, H. and D. Schroeder. 1993. The biological control of *Centaurea* spp. in North America: Do insects solve the problem? *Pesticide Science* 37: 343-353.

Müller, H., D. Schroeder, and A. Gassmann. 1988. *Agapeta zoegana* (L.) (Lepidoptera: Cochylidae), a suitable prospect for biological control of spotted and diffuse knapweed, *Centaurea maculosa* Monnet de la Marck and *Centaurea diffusa* Monnet de la Marck (Compositae) in North America. *Canadian Entomologist* 120: 109-124.

Müller, H., C. S. A Stinson, K. Marquardt, and D. Schroeder. 1989. The entomofaunas of roots of *Centaurea maculosa* Lam., *C. diffusa* Lam., and *C. vallesiaca* Jordan in Europe. *Journal of Applied Entomology* 107: 83-95

Rees, N. E., P. C. Quimby, Jr., G. L. Piper, E. M. Coombs, C. E. Turner, N. R. Spencer, and L. V. Knutson. (eds.). 1996. *Biological Control of Weeds in the West*. Western Society of Weed Science, Montana State University, Bozeman, Montana, USA.

Schroeder, D. 1985. The search for effective biological control agents in Europe. Diffuse and spotted knapweed, pp. 103-119. *In* Delfosse, E. (ed.). *Proceedings of the VI International Symposium on Biological Control of Weeds*. Vancouver, British Columbia, Canada.

Sheley, R. L., J. S. Jacobs, and M. E. Carpinelli. 1998. Distribution, biology, and management of diffuse knapweed (*Centaurea diffusa*) and spotted knapweed (*Centeaurea maculosa*). *Weed Technology* 12: 353-362.

Sobhian, R., G. Campobasso, and P. H. Dunn. 1992. A contribution to the biology of *Bangasternus fausti* (Col.:Curculionidae), a potential biological control agent of diffuse knapweed, *Centaurea diffusa*, and its effect on the host plant. *Entomophaga* 37: 171-179.

Stinson, C. S. A., D. Schroeder, and K. Marquardt. 1994. Investigations on *Cyphocleonus achates* (Fahr.) (Col., Curculionidae), a potential biological control agent of spotted knapweed (*Centaurea maculosa* Lam.) and diffuse knapweed (*C. diffusa* Lam.) (Compositae) in North America. *Journal of Applied Entomology* 117: 35-50.

Story, J. M., R. M. Nowierski, and K. W. Boggs. 1987. Distribution of *Urophora affinis* and *U. quadrifasciata*, two flies introduced for biological control of spotted knapweed (*Centaurea maculosa*) in Montana. *Weed Science* 35: 145-148.

Story, J. M., K. W. Boggs, and R. M. Nowierski. 1989. Effect of two introduced seed head flies on spotted knapweed. *Montana AgResearch* 6: 14-17.

Story, J. M., K. W. Boggs, W. R. Good, P. Harris, and R. M. Nowierski. 1991a. *Metzneria paucipunctella* Zeller (Lepidoptera: Gelechiidae), a moth introduced against spotted knapweed: its feeding strategy and impact on two introduced *Urophora* spp. (Diptera: Tephritidae). *Canadian Entomologist* 123: 1001-1007.

Story, J. M., K. W. Boggs, and W. R. Good. 1991b. First report of the establishment of *Agapeta zoegana* L. (Lepidoptera: Cochylidae) on spotted knapweed, *Centaurea maculosa* Lamarck, in the United States. *Canadian Entomologist* 123: 411-412.

Story, J. M., K. W. Boggs, and W. R. Good. 1992. Voltinism and phenological synchrony of *Urophora affinis* and *U. quadrifasciata* (Diptera: Tephritidae), two seed head flies introduced against spotted knapweed in Montana. *Environmental Entomology* 21: 1052-1059.

Story, J. M., W. R. Good, and L. J. White. 1997. First report of the establishment of *Cyphocleonus achates* (Fahraeus) (Coleoptera: Curculionidae) on spotted knapweed, *Centaurea maculosa* Lamarck, in the United States. *Canadian Entomologist* 129: 373-374.

Story, J. M., W. R. Good, L. J. White, and L. Smith. 2000. Effects of the interaction of the biocontrol agent, *Agapeta zoegana* L. (Lepidoptera: Cochylidae), and grass competition on spotted knapweed. *Biological Control* 17: 182-190.

Thompson, M. J. 1996. Winter foraging responses of elk to spotted knapweed removal. *Northwest Science* 70: 10-19.

Tyser, R. W. and C. H. Key. 1988. Spotted knapweed in natural area fescue grasslands: an ecological assessment. *Northwest Science* 62: 151-160.

USDA, NRCS. 2001. U.S. Department of Agriculture, Natural Resources Conservation Service. PLANTS Database. http://plants.usda.gov (accessed in 2001).

Watson, A. K. and A. J. Renney. 1974. The biology of Canadian weeds. *Centaurea diffusa* and *C. maculosa*. *Canadian Journal of Plant Science* 54: 687-701.

Wheeler, A. G. 1995. *Urophora quadrifasciata* (Diptera: Tephritidae), an introduced seedhead fly new to midwestern North America. *The Great Lakes Entomologist* 28: 235-236.

Wheeler, A. G. and C. A. Stoops. 1996. Establishment of *Urophora affinis* on spotted knapweed in Pennsylvania, with new eastern U.S. records of *U. quadrifasciata* (Diptera: Tephritidae). *Proceedings of the Entomological Society of Washington* 98: 93-99.

Zwölfer, H. 1970. Investigations on the host-specificity of *Urophora affinis* Frfld. (Dipt.: Trypetidae). Progress Report No. 25. Commonwealth Institute of Biological Control, Silwood Park, Berks, United Kingdom.