Compatibility of Seed Head Biological Control Agents and Mowing for Management of Spotted Knapweed

JIM M. STORY,[1] JANELLE G. CORN, AND LINDA J. WHITE

Montana Agricultural Experiment Station, Western Agricultural Research Center, 580 Quast Ln., Corvallis, MT 59828

Environ. Entomol. 39(1): 164–168 (2010); DOI: 10.1603/EN09123

ABSTRACT Field studies were conducted at two sites in western Montana during 2006 and 2008 to assess the compatibility of mowing with five seed head insect species introduced for biological control of spotted knapweed, *Centaurea stoebe* Lamarck subsp. *micranthos*. In 2006, mowing of spotted knapweed plants at the bolting and flower bud stages resulted in the development of new seed heads that contained significantly more seeds and significantly fewer larvae of each insect species than in seed heads in unmowed controls. No seed heads were produced in the plots mowed at the flowering stage. Seed numbers per seed head in 2008 were also significantly higher in plots mowed at the bolting stage than in unmowed controls, but between-treatment differences in insect numbers were more variable. The seed head insects *Larinus* spp. and *Urophora affinis* Frauenfeld were the primary cause of the reduced knapweed seed numbers per seed head in 2006. Spotted knapweed should not be mowed at the bolting and flower bud stages if large populations of seed head insects are present because mowing can result in the formation of new seed heads that are free from the insects' attack, thus allowing greater seed production. Mowing of spotted knapweed at the flowering stage and later can be conducted without a subsequent increase in seed production, but the mowing may cause mortality of the insect larvae.

KEY WORDS *Centaurea stoebe*, seed production, mowing, *Urophora affinis*, *Larinus* spp.

Spotted knapweed, *Centaurea stoebe* Lamarck subsp. *micranthos* (Gugler) Hayek (formerly *C. maculosa* Lamarck) (Ochsmann 2001), is a perennial plant from Eurasia that has become a serious weed on rangelands of the northwestern United States. First reported in North America in 1893 (Groh 1944), the plant now infests >3,000,000 ha of rangeland and pasture in 14 states and 2 Canadian provinces (Lacey 1989, Sheley et al. 1998). 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 reduces plant diversity (Tyser and Key 1988).

Many control options are effective against spotted knapweed, including herbicides, grazing, tillage, mowing, and biological control (Sheley et al. 1998; Duncan et al. 2001, Jacobs 2007). However, chemical and many cultural practices are often very expensive, temporary, and usually limited to accessible areas.

Considerable work has been conducted on the use of host-specific natural enemies to biologically control spotted knapweed. Twelve Eurasian insect species have been introduced into Montana and the Pacific Northwest for biological control of the plant. Of these, five species of seed-head insects are causing significant reductions in spotted knapweed seed production (Story et al. 1989, 1991, 2006, 2008; Smith and Mayer 2005; Seastedt et al. 2007). These insects include two seed head flies, *Urophora affinis* Frauenfeld and *U. quadrifasciata* (Meigen) (Diptera: Tephritidae), a seed head moth, *Metzneria paucipunctella* Zeller (Lepidoptera: Gelechiidae), and two seed head weevils, *Larinus obtusus* Gyllenhal and *L. minutus* Gyllenhal (Coleoptera: Curculionidae). A combination of *U. affinis* and the two *Larinus* spp. caused a 96% reduction in knapweed seed production in western Montana (Story et al. 2008).

Mowing has limitations but has been used with some success against noxious weeds. The method can prevent seed production, reduce carbohydrate reserves, and give competitive advantages to desirable perennial grasses (DiTomaso 2000, Jacobs 2007). Sheley (2002) reported that mowing of spotted knapweed at the flowering stage decreased mature plant density by ≈85%. Watson and Renney (1974) reported that the number of seed-producing spotted and diffuse knapweed plants was significantly reduced by mowing at the flower bud stage, the flowering stage, or at both the flower bud and flowering stage. Seed germination was significantly reduced by mowing at the flowering stage (Watson and Renney 1974). However, under favorable conditions, spotted knapweed will produce new flower buds after mowing. Story et al. (2008) reported that, because flower buds initiated after mowing gen-

[1] Corresponding author, e-mail: jstory@montana.edu.

erally develop after oviposition by the seed head insects is completed, those flower buds escape attack and thus produce a normal complement of seeds.

The objective of this study was to determine whether mowing could be timed so that any flower buds produced after mowing would not escape attack by the seed head insects. We predicted that flower buds produced on plants mowed at the bolting, flower bud, or flowering stages would escape insect attack and thus produce a full complement of seeds.

Materials and Methods

The study was conducted at two sites in western Montana during 2006 and 2008. The study was conducted at the Montana State University–Western Agricultural Research Center (WARC), Corvallis, MT, during both years. The study was also conducted at a field site in 2006 (Unrue, Corvallis, MT).

WARC. The WARC site, located 3.2 km northeast of Corvallis, was a level, arable field. In 2006, treatment plots were established within a large (64 by 41 m) spotted knapweed garden that received some irrigation during the growing season. Each plot consisted of a 7-m portion of a row in the knapweed garden, with each plot randomly located in a different row. Spotted knapweed plants were mowed in five plots on one of three dates representing different developmental stages: 8 June (bolting stage), 29 June (flower bud stage), and 20 July (flowering stage), for a total of 20 plots (including 5 unmowed control plots). Mowing at the bolting stage occurred when >80% of the plants were bolting, whereas mowing at the flower bud and flowering stages was conducted when >50% of the plants contained flower buds or flowers, respectively. Mowing consisted of cutting the plants 15 cm above ground with hedge shears. Fifty spotted knapweed seed heads were randomly collected from each of the five unmowed controls on 3 August, just before the seed heads opening for seed dispersal. The two nearest seed heads on every fourth plant were collected along a transect through the plots until a total of 50 seed heads had been collected. Similarly, because of the mowing-caused delay in development of the seed heads, 50 seed heads were randomly collected on 15 August from each of the five plots mowed at the bolting stage and on 18 August from the five plots mowed at the flower bud stage. No flower buds were produced in the plots mowed at the flowering stage. The collected seed heads were individually stored in small envelopes in the laboratory until October, when the seed heads were examined under a dissecting microscope to determine seed numbers and numbers of five seed head insect species: *U. affinis*, *U. quadrifasciata*, *M. paucipunctella*, *L. obtusus*, and *L. minutus*. Because it was very difficult to distinguish between the two *Larinus* species, *Larinus* individuals are hereafter referred to as *Larinus* spp.

Procedures used at WARC in 2008 were similar to 2006, but the spotted knapweed garden was smaller (21 by 11 m) and did not receive irrigation. Five plots were mowed on 6 June (bolting stage), five were mowed on 30 June flower bud stage, five were mowed on 21 July (flowering stage), and five plots were not mowed. Fifty seed heads were collected per unmowed control plots on 29 July, whereas available seed heads from the plots mowed in the bolting stage were collected on 1 and 4 August. No flower buds were produced in the plots mowed at the flower bud and flowering stages.

Unrue. The Unrue site was a natural spotted knapweed infestation on a south-facing slope, located 3.2 km east of Corvallis. In 2006, five 7 by 1-m strips were mowed at a 15-cm height with hedge shears on 3 July at the flower bud stage. Fifty seed heads from each of five unmowed strips were randomly collected on 4 August, whereas 50 seed heads from each of the five mowed plots were similarly collected on 28 August. The seed heads were processed in the laboratory using the above-mentioned procedures. This site received only natural precipitation.

Statistical Analysis. Spotted knapweed seed numbers and insect numbers per seed head were analyzed by analysis of variance (ANOVA) procedures, and means were compared using least significant difference (LSD; Statistix 8 2003). The data were transformed by $\sqrt{(y + 0.5)}$ before the ANOVA to improve normality (Sokal and Rohlf 1981). Multiple regression analysis was used to describe the relationship between individual insect species numbers and seed numbers per seed head.

Results and Discussion

WARC. In 2006, spotted knapweed seed numbers per seed head in plots mowed at the bolting stage (8 June) and the flower bud stage (29 June) were significantly higher than in unmowed controls ($F = 111.0$; df = 2,12; $P < 0.001$; Table 1). Seed numbers per seed head in the plots mowed at the bolting stage were significantly higher than in plots mowed at the flower bud stage. As previously mentioned, no flower buds were produced in the plots mowed at the flowering stage. The numbers of each of the four insect species and all four insect species combined (total insects) per seed head were significantly higher in the unmowed control plots than in the mowed plots(for *U. affinis*, $F = 38.8$; df = 2,12; $P < 0.001$; for *U. quadrifasciata*, $F = 8.7$; df = 2,12; $P = 0.005$; for *Larinus* spp., $F = 17.4$; df = 2,12; $P < 0.001$; for M. paucipunctella, $F = 7.4$; df = 2,12; $P = 0.008$; and for total insects, $F = 52.5$; df = 2,12; $P < 0.001$). Overall, numbers of individual insect species were similar between the two mowing dates. Results of multiple regression analysis indicated that each *Larinus* spp. individual reduced spotted knapweed seed production by 11.5 ± 0.5 seeds per seed head compared with 8.0 ± 1.5 seeds for *M. paucipunctella*, 3.1 ± 0.6 seeds for *U. quadrifasciata*, and 2.1 ± 0.2 seeds for *U. affinis* ($Y = 23.3 - 11.5X_1 - 8.0X_2 - 3.1X_3 - 2.1X_4$, where Y = seed production, X_1 = *Larinus* spp., X_2 = *M. paucipunctella*, X_3 = *U. quadrifasciata*, and X_4 = *U. affinis*; $R^2 = 0.54$; $P < 0.001$).

Table 1. Comparison of seed and insect numbers per seed head among mowing stages (mean ± SEM)

Site-year	Mowing stage	Seeds per seed head	Insect numbers per seed head				
			Urophora affinis	*Urophora quadrifasciata*	*Larinus* spp.	*Metzneria paucipunctella*	Total insects
WARC-06	Bolt	23.6 ± 1.0a	0.08 ± 0.02b	0.03 ± 0.01b	0.4 ± 0.04b	0.007 ± 0.007b	0.5 ± 0.04b
	Bud	19.0 ± 1.3b	0.05 ± 0.03b	0.04 ± 0.03b	0.4 ± 0.08b	0.008 ± 0.008b	0.5 ± 0.1b
	Control	5.4 ± 0.6c	1.7 ± 0.3a	0.2 ± 0.05a	0.8 ± 0.04a	0.1 ± 0.03a	2.9 ± 0.3a
Unrue-06	Bud	14.6 ± 1.2a	0.03 ± 0.03b	1.3 ± 0.1a	0.2 ± 0.04a	0b	1.6 ± 0.09b
	Control	7.5 ± 0.5b	2.3 ± 0.2a	1.5 ± 0.05a	0.3 ± 0.04a	0.2 ± 0.02a	4.4 ± 0.2a
WARC-08	Bolt	10.9 ± 0.9a	0.1 ± 0.03b	0.04 ± 0.01a	1.7 ± 0.04a	0.005 ± 0.003a	1.8 ± 0.06a
	Control	7.6 ± 1.3b	0.6 ± 0.1a	0.06 ± 0.01a	1.2 ± 0.07b	0.005 ± 0.005a	1.9 ± 0.1a

Means within a column for each site followed by the same letter are not significantly different at the $P < 0.05$ level.

In 2008, spotted knapweed seed numbers per seed head in plots mowed at the bolting stage (6 June) were significantly higher than in unmowed controls (F = 4.6; df = 1,23; P = 0.04; Table 1). No flower buds were produced in the plots mowed at the flower bud and flowering stages. *U. affinis* numbers were significantly higher in the unmowed controls than in the mowed plots (F = 25.7; df = 1,23; $P < 0.001$), whereas *Larinus* spp. numbers were significantly lower in the unmowed controls than in the mowed plots (F = 37.9; df = 1,23; $P < 0.001$). The numbers of *U. quadrifasciata, M. paucipunctella,* and total insects were not significantly different between mowed and unmowed plots ($P > 0.05$). Results of multiple regression analysis indicated that the seed head insects explained very little of the variability in seed production ($R^2 = 0.04$, $P < 0.001$).

A comparison of the WARC 2006 and 2008 data from the unmowed controls and plots mowed at the bolting stage indicated that seed numbers per seed head were not different between years among unmowed controls, but seed numbers per seed head were significantly higher in the mowed plots in 2006 than in 2008 (F = 32.6; df = 1,18; $P < 0.001$). Overall, numbers of *U. affinis, U. quadrifasciata,* and *M. paucipunctella* were significantly higher in 2006 than in 2008 (for *U. affinis,* F = 4.9; df = 1,33; P = 0.03; for *U. quadrifasciata,* F = 7.2; df = 1,33; P = 0.01; for *M. paucipunctella,* F = 11.5; df = 1,33; P = 0.002). Numbers of *Larinus* spp., however, were significantly higher in 2008 (F = 74.1; df = 1,33; $P < 0.001$).

Unrue. Spotted knapweed seed numbers per seed head in plots mowed at the flower bud stage (3 July) in 2006 were significantly higher than in unmowed controls (F = 35.4; df = 1,7; $P < 0.001$; Table 1). Numbers of *U. affinis, M. paucipunctella,* and total insects per seed head were significantly higher in the unmowed controls than in the mowed plots (for *U. affinis,* F = 133.0; df = 1,7; $P < 0.001$; for *M. paucipunctella,* F = 151.0; df = 1,7; $P < 0.001$; for total insects, F = 129.0; df = 1,7; $P < 0.001$). The numbers of *U. quadrifasciata* and *Larinus* spp. per seed head were not significantly different between mowed and unmowed plots ($P > 0.05$). Results of multiple regression analysis indicated that each *Larinus* spp. individual reduced spotted knapweed seed production by 6.8 ± 0.8 seeds per seed head compared with 5.7 ± 1.1 seeds for *M. paucipunctella,* 1.7 ± 0.2 seeds for *U. quadrifasciata,* and 1.1 ± 0.2 seeds for *U. affinis* ($Y = 17.2 - 6.8X_1 - 5.7X_2 - 1.7X_3 - 1.1X_4$, where Y = seed production, X_1 = *Larinus* spp., X_2 = *M. paucipunctella,* X_3 = *U. quadrifasciata,* and X_4 = *U. affinis;* $R^2 = 0.43$; $P < 0.001$).

The seed data generally supported our hypothesis relative to those mowing times that yielded data. Mowing of spotted knapweed plants at the bolting and flower bud stage at WARC in 2006, the flower bud stage at Unrue, and the bolting stage at WARC in 2008 resulted in the development of new flower buds that largely escaped attack by the seed head insects and thus produced a significantly higher number of seeds per seed head than in unmowed controls. Seed production in seed heads from the mowed plots was less than that of unattacked plants historically (Story 1976), because some flower buds in the mowed plots were attacked by the seed head insects. Normal seed production in seed heads of unattacked spotted knapweed plants is ≈30 seeds per seed head (Story 1976, Story et al. 2008). Our results from mowing at the flowering stage supported Sheley (2002), who reported that mowing at that stage effectively reduced seed production, but our lack of seed production was caused by the complete absence of seed heads. Reasons why seed heads were not produced in plots mowed at the flowering stage at WARC in 2006 and at the flower bud and flowering stages at WARC in 2008 were not determined but were probably caused by dry conditions.

The seed head insects were the primary cause of the low seed numbers per seed head in unmowed controls at WARC and Unrue in 2006. Numbers of all insect species were significantly higher in the unmowed controls than in the mowed plots at WARC. At Unrue, the number of *U. affinis* and total insects was significantly higher in the unmowed controls than in the mowed plots. Because of low numbers of both seeds and insects per seed head at WARC in 2008, no relationship among seed and insect numbers was evident during that year.

Of the five seed-head insects, the *Larinus* spp. and *U. affinis* had the greatest impact on spotted knapweed seed production. Based on the WARC 2006 data, each *Larinus* spp. larva reduced seed production by ≈11.5 seeds per seed head, whereas each *U. affinis* larva reduced seed production by about two seeds per seed head. However, the lower seed reduction of *U. affinis* was offset somewhat by its greater abundance at all sites except WARC in 2008, where *Larinus* spp. were more abundant. Seed reductions by *U. affinis* were probably an underestimate of its total impact because galls of *U. affinis* act as strong metabolic sinks that can reduce seed production in both attacked and unattacked seed heads and may suppress development of other seed heads and reduce vegetative grown (Harris 1980, Harris and Shorthouse 1996). The trend in seed reductions by *Larinus* spp. and *U. affinis* was similar at Unrue, but the number of seeds reduced by each insect species was less. Because of very low population numbers, *U. quadrifasciata* and *M. paucipunctella* had little impact at all study sites.

The seed numbers per seed head in the plots mowed at the bolting stage at WARC in 2008 were significantly less than plots mowed at the bolting stage at WARC in 2006. The low seed numbers per seed head in 2008 was probably caused primarily by the high numbers of *Larinus* spp. per seed head (1.7) in the mowed plots. Using the seed reduction estimates of *Larinus* spp. at WARC 2006 (11.5 seeds per weevil), *Larinus* spp. could have potentially reduced seed production in the mowed plots at WARC in 2008 by 19.5 seeds per seed head. Reduced precipitation may have also contributed to the lower seed numbers per seed head in 2008; precipitation during January through July in 2008 (10.1 cm) was less than the same period in 2006 (14.7 cm), but the precipitation difference does not seem to be enough to explain the difference in seed numbers. Reduced pollination may also have been a factor as few pollinators were observed in spotted knapweed flowers in 2008 in contrast to previous years, but no data were collected to evaluate that factor. The presence of two root-feeding spotted knapweed biological control agents, *Agapeta zoegana* L. (Lepidoptera: Tortricidae) and *Cyphocleonus achates* (Fahraeus) (Coleoptera: Curculionidae), may have contributed to the low seed numbers in 2008. However, comparisons of those insects' populations were not made between years.

In addition to having unexpectedly high numbers of *Larinus* spp. in the mowed plots, WARC in 2008 also contained very low numbers of the other insect species in unmowed controls. Reasons for the low numbers of *U. affinis* and *U. quadrifasciata* in 2008 were not determined but could be a combined result of declining spotted knapweed populations in the study area (Story et al. 2006, 2008) and predation (Story et al.1995). The high *Larinus* spp. numbers at WARC in 2008 may reflect the fact that it overwinters in the soil and thus escapes rodent predation. The fact that *Larinus* spp. numbers were higher in mowed plots at WARC 2008 (bolting stage) may reflect an unusually late emergence of the adults.

Research on the effects of mowing on spotted knapweed seed production has been limited, but Sheley (2002) reported that mowing at the flowering stage effectively reduced seed production. However, mowing of small spotted knapweed infestations is often conducted at the bolting and flower bud stages for esthetic purposes. Mowing of spotted knapweed at these stages probably also reduces seed production if follow-up mowings are conducted every few weeks throughout the growing season before the flowering stage, but multiple mowings are usually not conducted.

Our results might have been somewhat different if we had used a conventional mower instead of hedge shears. Conventional mowers would likely have cut the knapweed closer to the ground, which might have altered the plants' response to the mowing. Regardless of the mowing height, however, spotted knapweed will produce secondary seed heads if mowed in spring and early summer (J.M.S., unpublished data).

Single mowings at the bolting or flower bud stages in the years before the establishment of the seed head biocontrol insects did not alter spotted knapweed seed production; seed numbers were high on both mowed and unmowed plants (J.M.S., unpublished data). Now, however, the seed head biocontrol insects are reducing spotted knapweed seed production by up to 94% in many areas of western Montana (Story et al. 2008), and mowing at the wrong time can allow the production of flower buds that escape this high level of insect attack and thus produce a nearly full complement of seeds. Based on our 2006 results, we conclude that the historical practice of mowing spotted knapweed during the bolting or flower bud stage with no follow-up mowings should be avoided if large populations of seed head biocontrol agents are present. Mowing of spotted knapweed at the flowering stage in areas with high seed head biocontrol insect populations can be conducted for esthetic purposes without a subsequent increase in seed production. Mowing anytime after the flowering stage can result in mortality of seed head insect larvae present within the seed heads (Story et al. 1988), but adults of seed head insects will be present in the area in the following June if ample numbers of the insects occur in adjacent areas.

Acknowledgments

We thank A. Knudsen, L. Maclay, C. Tintzman, and K. Paulsen for assistance. Partial support was provided by the Bureau of Indian Affairs, the Bureau of Land Management, the U.S. Forest Service, and numerous western Montana counties. This report is based in part on research conducted and supported as a part of SAES Western Regional Research Project, W-2185.

References Cited

DiTomaso, J. M. 2000. Invasive weeds in rangelands: species, impacts, and management. Weed Sci. 48: 255–265.

Duncan, C., J. Story, and R. Sheley. 2001. Montana knapweeds: identification, biology and management. Montana Coop. Ext. Serv. Circular No. 311.

Groh, H. 1944. Canadian weed survey, 2nd annual report. Canada Department of Agriculture, Ottawa, Canada.

Harris, P. 1980. Effects of *Urophora affinis* Frfld. and *U. quadrifasciata* (Meig.) (Diptera: Tephritidae) on *Centaurea diffusa* Lam. and *C. maculosa* Lam. (Compositae). Zeitschrift Angewandte Entomol. 90: 190–201.

Harris, P., and J. D. Shorthouse. 1996. Effectiveness of gall inducers in weed biological control. Can. Entomol. 128: 1021–1055.

Jacobs, J. 2007. Ecology and management of spotted knapweed (*Centaurea maculosa* Lam.). U.S. Department of Agriculture–Natural Resources Conservation Service.

Lacey, C. 1989. Knapweed management: a decade of change, pp. 1–6. *In* P. Fay and J. Lacey (eds.), Proceedings of the 1989 Knapweed Symposium, 4–5 April 1989, Bozeman, MT. Montana State University, Bozeman, MT.

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

Ochsmann, J. 2001. On the taxonomy of spotted knapweed (*Centaurea stoebe* L.), pp. 33–41. *In* L. Smith (ed.), Proceedings of the First International Knapweed Symposium of the Twenty-First Century, 15–16 March 2001, Coeur d'Alene, ID. USDA–ARS, Albany, CA.

Seastedt, T. R., D. G. Knochel, M. Garmoe, and S. A. Shosky. 2007. Interactions and effects of multiple biological control insects on diffuse and spotted knapweed in the Front Range of Colorado. Biol. Control 42: 345–354.

Sheley, R. 2002. Mowing to manage noxious weeds. MontGuide #200104. Montana State University Extension Service, Bozeman, MT.

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

Smith, L., and M. Mayer. 2005. Field cage assessment of interference among insects attacking seed heads of spotted and diffuse knapweed. Biocontrol Sci. Technol. 15: 427–442.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. The principles and practice of statistics in biological research. W.H. Freeman and Co., San Francisco, CA.

Statistix 8. 2003. Analytical Software, Tallahassee, FL.

Story, J. M. 1976. A study of *Urophora affinis* (Diptera: Tephritidae) released on spotted knapweed in western Montana. MS thesis, Montana State University, Bozeman, MT.

Story, J. M., K. W. Boggs, W. R. Good, and R. M. Nowierski. 1988. 2,4-D and mowing effects on seed-head flies used for spotted knapweed control. Mont. AgRes. 5: 8–11.

Story, J. M., K. W. Boggs, and R. M. Nowierski. 1989. Effect of two introduced seed head flies on spotted knapweed. Mont. AgRes. 6: 14–17.

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

Story, J. M., K. W. Boggs, W. R. Good, L. J. White, and R. M. Nowierski. 1995. Cause and extent of predation on *Urophora* spp. larvae (Diptera: Tephritidae) in spotted knapweed capitula. Environ. Entomol. 24: 1467–1472.

Story, J. M., N. W. Callan, J. G. Corn, and L. J. White. 2006. Decline of spotted knapweed density at two sites in western Montana with large populations of the introduced root weevil, *Cyphocleonus achates* (Fahraeus). Biol. Control 38: 227–232.

Story, J. M., L. Smith, J. G. Corn, and L. J. White. 2008. Influence of seed head-attacking biological control agents on spotted knapweed reproductive potential in western Montana over a 30-year period. Environ. Entomol. 37: 510–519.

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

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

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

Received 22 April 2009; accepted 11 September 2009.