Compatibility of Two Herbicides with *Cyphocleonus achates* (Coleoptera: Curculionidae) and *Agapeta zoegana* (Lepidoptera: Tortricidae), Two Root Insects Introduced for Biological Control of Spotted Knapweed

J. M. STORY[1] AND R. N. STOUGAARD[2]

Environ. Entomol. 35(2): 373–378 (2006)

ABSTRACT Field studies were conducted in 2001 through 2004 to assess the compatibility of two herbicides, 2,4-D (2,4-dichlorophenoxyacetic acid) and clopyralid (3,6-dichloropicolinic acid), with two root insects, *Cyphocleonus achates* (Fahraeus), and *Agapeta zoegana* L., introduced for biological control of spotted knapweed, *Centaurea stoebe* Lamarck subsp. *micranthos* (formerly *C. maculosa*) in Montana. Both herbicides were applied at the fall and spring rosette stage. In 2003, both herbicides reduced knapweed canopy cover by ≈98% compared with ≈85% in 2004. The number of live larvae of both insect species was significantly lower in treated plots than in controls in 2003. In 2004, the number of live *C. achates* larvae was significantly lower in treated plots than in controls at the fall application, but larval numbers were not different at the spring application. Larval numbers of *C. achates* were not different between application times in 2003 but were significantly lower in fall-treated plots than in spring-treated plots in 2004. Numbers of *A. zoegana* larvae were not different between treated plots and controls in 2004. Larval numbers of *A. zoegana* were significantly lower in fall-treated plots than in spring-treated plots in 2003, but there was no difference between application times in 2004. Larval numbers of each insect species were similar between herbicides in both years. We conclude that fall applications of both herbicides are not compatible with the two insects. Spring applications of the two herbicides may be compatible with both insect species if delayed until late spring.

KEY WORDS *Cyphocleonus achates*, *Agapeta zoegana*, *Centaurea maculosa*, biological control, herbicides

SPOTTED KNAPWEED, *Centaurea stoebe* Lamarck ssp. *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 run-off and soil sedimentation (Lacey et al. 1989), and reduces plant diversity (Tyser and Key 1988).

Land managers use various strategies to manage spotted knapweed. The weed is readily controlled by some herbicides (Duncan et al. 2001), but their use is often limited because of expense, environmental concerns, impacts on nontarget plants, and logistical constraints. Biological control, the use of natural enemies to manage the weed, avoids some of these problems, and has been in use against spotted knapweed in North America since the early 1970s.

A Eurasian root-mining moth, *Agapeta zoegana* L. (Lepidoptera: Tortricidae), and a Eurasian root-mining weevil, *Cyphocleonus achates* (Fahraeus) (Coleoptera: Curculionidae), have been introduced into North America for biological control of spotted knapweed. The first U.S. release of the moth was made in Montana in 1984, whereas the first release of the weevil occurred in Montana in 1988 (Story et al. 1991, 1997). Both insects are now established at many sites in western Montana (Story and Piper 2001). The moth is causing reductions of knapweed biomass at some sites (Story et al. 2000), and the weevil is causing declines in knapweed density (J.M.S., unpublished data).

The biology of *A. zoegana* was described by Müller et al. (1988) and Müller (1989). Early-instar larvae mine the epidermal tissues of the root crown, whereas older larvae mine the epidermal and cortex tissues. The moth larvae overwinter in the root, resume feeding in the spring, and emerge as adults between mid-June and mid-September, with peak emergence oc-

[1] Corresponding author: MSU/Western Agric. Research Center, 580 Quast Ln., Corvallis, MT 59828 (e-mail: mailto:jstory@montana.edu).

[2] Montana Agricultural Experiment Station, Northwestern Agricultural Research Center, Creston, MT 59902.

0046-225X/06/0373–0378$04.00/0 © 2006 Entomological Society of America

curring in early August in western Montana (Story et al. 1991). Females lay 150–400 eggs, generally within a 3- to 4-d period. The moth apparently has only one generation per year in Montana.

The biology of *C. achates* was described by Stinson et al. (1994). Larvae mine the root cortex, generally in the top 6 cm of the root. The larvae feed during late summer and fall, overwinter in the root, resume feeding in the spring, and emerge as adults between mid-July and mid-September. Peak adult emergence occurs in mid-August in Montana (Story et al. 1997). Each female lays 1–3 eggs/d on knapweed root crowns. Adults live for 8–15 wk. The weevil has one generation per year.

Biological control will not be the total answer to knapweed management because it also has limitations. Long-term, cost-effective management of spotted knapweed may benefit from an integrated approach involving both herbicides and biological control. Attempts to assess the compatibility of herbicides with insects introduced as biological control agents have been increasing as more insect species are introduced and established against target weeds (Trumble and Kok 1979, 1980a, b, Haag 1986, Rees and Fay 1989, Lym and Carlson 1994, Lym and Nelson 2002). Story et al. (1988) and McCaffrey and Callihan (1988) reported on the integration of herbicides with two seed head flies (*Urophora* spp.) introduced against spotted knapweed. Jacobs et al. (2000) evaluated the effect of the herbicide, picloram, on the establishment of *C. achates.*

Most herbicides can be applied at several spotted knapweed phenological development stages. However, applications made at the rosette stage of development, either during the fall or spring, are generally most effective because the plants are smaller, and the timing typically coincides with periods of high rainfall that improves herbicide translocation. In addition, applications made during the rosette stage minimize the weed's competitive effect on associated vegetation.

The larvae of both insects are actively feeding during the fall and spring rosette stages. Thus, understanding whether herbicide applications at these optimal spray times would allow *A. zoegana* and *C. achates* to complete their life cycle is important. This paper reports the impacts of fall and spring applications of 2,4-D and clopyralid on the larvae of the two insects, *A. zoegana* and *C. achates*, occurring within the knapweed roots.

Materials and Methods

The study was conducted during 2001 through 2004 in a tilled field at the MSU/Western Agricultural Research Center, near Corvallis, MT. In the spring of 2001, 25 small knapweed rosettes (roots ≈5–10 mm diameter), collected from a remote site, were transplanted into each of 30 1.2 by 1.2-m plots, using a between- and within-row spacing of 30 cm. The plots were positioned in a 16 by 13-m tract with 1.2-m alleys between plots. The plants were watered at the time of planting and semiweekly for several weeks thereafter until the plants were established. In 2002, volunteer knapweed plants were also present in the plots.

The knapweed plants in the plots were purposely exposed to infestation by *A. zoegana* and *C. achates.* Infestation by the moth occurred naturally in July and August 2001 because the strong-flying adults were very prevalent in the area. However, *C. achates* adults do not fly, so infestation of the plots required confinement of adults by placing a corral around the entire tract. The corral was made of aluminum flashing (25 cm in height), held in place by 60-cm wooden stakes placed every 1.2 m around the outside edge of the corral (Story et al. 1996). The lower 5 cm of the flashing was inserted below the soil surface. The upper 5 cm of the flashing was folded downward toward the inside of the corral to prevent weevil escape. In early August 2001, 300 adult weevils were placed in the corral.

The factorial treatment arrangement consisted of two herbicides (2,4-D ester and clopyralid) and two application timings (fall and spring rosette stages) established in a randomized complete block design with five replications. Nontreated controls were included for both fall and spring application timings. Clopyralid and 2,4-D were applied with a pressurized backpack sprayer at the rate of 0.28 and 2.24 (AI) kg/ha, respectively, in 187 liters water/ha.

To allow for adequate establishment of *C. achates*, herbicide applications were not initiated until 13 mo after the insect's release. Herbicide application was made at the fall rosette growth stage on 26 September 2002 and at the spring rosette growth stage on 15 May 2003. The experiment was repeated in spring 2002 with a new planting of spotted knapweed, using the procedures previously described. Herbicide applications for the repeat experiment were made on 23 September 2003 and 14 May 2004. The plots sprayed in fall of 2002 and spring of 2003 will be referred to as the 2003 experiment while the plots sprayed in fall of 2003 and spring of 2004 will be called the 2004 experiment.

The roots of five knapweed plants that had been present in the plots the previous year were randomly selected from each plot, dug up in mid-June of each year, and dissected in the laboratory to determine the number of live individuals and life stages of both insect species. The results of the five plants were pooled, producing a mean per plant for each plot. Because of the differences in herbicide effect during the two years, all of the plants sampled in the 2003 plots were dead, while many of the plants sampled in the 2004 plots were alive or moribund. The herbicide effects on the knapweed plants were assessed by estimating knapweed canopy cover in the plots in May for fall spray plots and in July for spring spray plots.

Univariate analysis and a plot of residuals indicated that the knapweed canopy cover data were normally distributed. Data were analyzed by analysis of variance (ANOVA) procedures, and means were compared using Fischer's protected least significant difference (LSD) (SAS Institute 1999). Because of treatment by year interactions, 2003 and 2004 data were analyzed separately.

Table 1. Main effect of herbicides and application date on spotted knapweed canopy cover and larval numbers of two root-feeding insects in 2003

Variable	Percent reduction in knapweed cover	Mean ± SEM no. live larvae/plant	
		Cyphocleonus achates	*Agapeta zoegana*
Treatment			
Clopyralid	99 ± 0.67a	0.33 ± 0.20a	1.8 ± 0.68a
2,4-D	98 ± 0.66a	0.04 ± 0.03a	2.7 ± 0.72a
Control	0b	5.9 ± 1.11b	7.1 ± 0.74b
LSD	1.66	1.92	1.65
Timing			
Fall	66 ± 12.4a	2.1 ± 0.97a	2.7 ± 0.87a
Spring	66 ± 12.5a	2.1 ± 0.78a	5.0 ± 0.68b
LSD	NS	NS	1.34

Means within columns for each parameter followed by the same letter are not significantly different at the $P < 0.05$ level.
NS, not significant.

Results and Discussion

The effects of the herbicides on knapweed and two insect species in 2003 and 2004 are shown in Tables 1 and 2, respectively. The data format for Table 2 is different from Table 1 because of a significant herbicide and application timing interaction in the 2004 data. The interaction in 2003 was not significant.

Effect of Herbicide Applications on Spotted Knapweed. Both herbicides caused extensive knapweed canopy cover reduction in the 2003 experiment ($F = 10558.8$; df = 2,22; $P < 0.0001$), reducing knapweed cover by ≈98% (Table 1). Both herbicides caused similar reductions in knapweed canopy cover regardless of the application timing. Conversely, the two herbicides caused extensive knapweed canopy cover reductions in 2004 ($F = 402.9$; df = 2,22; $P < 0.0001$), but the efficacy of the two herbicides was more variable (Table 2). Fall applications of 2,4-D were less effective than clopyralid applications in controlling spotted knapweed in 2004. Fall-applied clopyralid reduced knapweed canopy cover by 91% compared with 76% for 2,4-D. However, both herbicides provided similar levels of knapweed control when applied in the spring, resulting in a herbicide by application timing interaction (Table 2). Spring-applied clopyralid reduced knapweed canopy cover by 83% compared with 89% for 2,4-D. The decreased herbicide effectiveness in the 2004 experiment may have been a result of the unusually dry fall and spring conditions (Fig. 1). Less than 1 cm of precipitation was received during September 2003 when fall applications were made. In addition, the only significant precipitation in the first 5 mo of 2004 (3 cm) occurred just 2 d before the spring applications were made. The impact of water stress on herbicide translocation has been documented. Morrison et al. (1995) reported on reduced herbicide translocation and poor control of Russian knapweed as a result of water stress.

Table 2. Interactions of application date and herbicides on spotted knapweed canopy cover and larval numbers of two root-feeding insects in 2004

Timing	Treatment	Percent reduction in knapweed cover	Mean ± SEM no. live larvae/plant	
			Cyphocleonus achates	*Agapeta zoegana*
Fall	Clopyralid	91 ± 3.44a	0c	0.48 ± 0.23a
	2,4-D	76 ± 4.85b	0.68 ± 0.47c	1.28 ± 0.46a
	Control	0c	7.0 ± 1.79a	2.40 ± 0.83a
Spring	Clopyralid	83 ± 2.0ab	6.88 ± 3.03ab	2.04 ± 0.91a
	2,4-D	89 ± 1.0a	2.76 ± 0.65cb	1.96 ± 0.73a
	Control	0c	5.84 ± 1.75ab	2.00 ± 1.04a
	(LSD)	8.15	4.21	NS

Means within columns followed by the same letter are not significantly different at the $P < 0.05$ level.
NS, not significant.

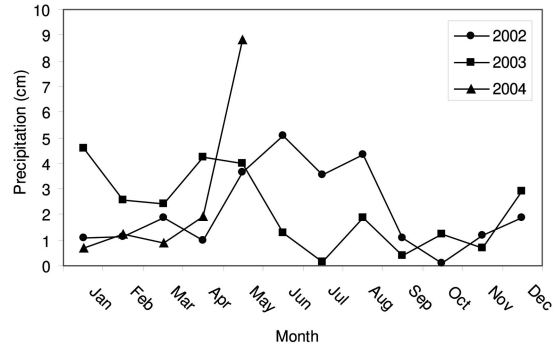

Fig. 1. Monthly precipitation at the study site from January 2002 to May 2004.

Many (≈40%) of the knapweed plants, especially large plants, died over winter in the spring 2004 plots before herbicide application. Reasons for the mortality are unknown, but were possibly caused by a combination of higher numbers of *C. achates* and drought stress during the previous growing season. Numbers of *C. achates* were not controllable in the second summer after introduction, so large plants could have had inordinately high larval numbers in late 2003, causing excessive stress and subsequent mortality to the plants during the winter. The summer of 2003 (May–September) received only 7.6 cm of precipitation compared with 17.7 cm in 2002 (Fig. 1).

Effect of Herbicide Applications on *C. achates*. The number of *C. achates* larvae per plant in control plots was significantly higher than in treated plots in the 2003 experiment ($F = 27.08$; df = 2,22; $P < 0.0001$; Table 1). Overall, larval numbers were similar between herbicides and between application times in 2003. Herbicides also had an effect on larval numbers in the 2004 experiment ($F = 5.53$; df = 2,20; $P = 0.01$), but insect mortality varied by herbicide and application timing, resulting in a significant two-way interaction ($F = 4.0$; df = 2,20; $P = 0.03$). In 2004, the number of live *C. achates* larvae was significantly lower in treated plots than in control plots in the fall application, but there was no difference between treated plots and controls in the spring application (Table 2). Larval numbers were similar between herbicides in 2004. Larval numbers were significantly lower in fall

plots than in spring in 2004 ($F = 4.96$; df = 1,20; $P = 0.04$).

Vigor of *C. achates* larvae was highly dependent on the health of the knapweed plants. If the herbicides killed the knapweed plants, weevil larvae generally did not survive, regardless of the application date. This response was most apparent with fall herbicide applications. Fall application of both herbicides caused high knapweed mortality that, in turn, caused high larval mortality in both years. However, results of the spring application were more variable. In the 2003 experiment, spring application of both herbicides caused high knapweed mortality and *C. achates* larval mortality. In the 2004 experiment, knapweed canopy cover reduction in clopyralid plots was similar at both application times, but larval numbers were significantly higher in spring plots compared with fall. While not statistically significant, results with 2,4-D applications during 2004 showed the same trend.

Overall, larval numbers per plant documented in the 2004 experiment were much higher than those from the 2003 experiment (Table 1 and 2). The increased survival of *C. achates* larvae in 2004 was a result of decreased effectiveness of the herbicides, especially clopyralid, in the spring. Also, many of the knapweed plants in the spring spray plots may have been more viable than the canopy cover estimate would suggest. Although many of the plants appeared to be moribund at the time of plant harvest (i.e., they were severely distorted and stunted), they may actually have been sufficiently viable to allow larval survival.

Effect of Herbicide Applications on *A. zoegana*. The number of *A. zoegana* larvae per plant in control plots was significantly higher than in treated plots in 2003 ($F = 22.84$; df = 2,22; $P < 0.0001$) but were not different in 2004 (Tables 1 and 2). Overall, larval numbers were similar in plots sprayed with either of the two herbicides in 2003. However, larval numbers in spring plots were significantly higher than in fall plots in 2003 ($F = 11.07$; df = 1,22; $P = 0.003$; Table 1). Larval numbers were not affected by herbicide or application timing in 2004 (Table 2). Overall, larval numbers in 2003 were higher than in 2004.

Knapweed mortality resulted in death of most *A. zoegana* larvae, although a small number did survive in dead plants. The lack of a treatment effect in 2004 was likely caused by the reduced effectiveness of the herbicides. Fall application of both herbicides caused high knapweed mortality that, in turn, caused high mortality of *A. zoegana* larvae in 2003, but not in 2004. In 2003, high knapweed mortality occurred in the spring spray plots but many larvae survived; however, live larval numbers were not different between dates in 2004.

Results of the spring herbicide applications were somewhat surprising. We expected larval survival of both insect species to be higher in spring spray plots than in fall plots because of the greater maturity of the larvae at the spring application date. That scenario did occur in 2003 for *A. zoegana*, but not for *C. achates*, whereas in 2004, the reverse occurred (Tables 1 and 2). In 2004, *C. achates* survival was significantly higher in the spring plots, whereas *A. zoegana* larval numbers were not different. The lack of a difference in *A. zoegana* larval numbers between application times in 2004 was likely caused by the reduced efficacy of the herbicides, as mentioned above. Reasons for the low *A. zoegana* population in both the fall and spring plots in 2004 were not determined, but population reductions appeared to be widespread. Mean *A. zoegana* larval numbers per plant in control plots were 7.06 ± 0.74 (SEM) in 2003 compared with 2.2 ± 0.63 in 2004. The higher *C. achates* numbers in spring 2004, compared with fall, were likely also a result of the ineffectiveness of the two herbicides. It is possible that our sampling of the larvae in the moribund plants was premature; the live *C. achates* larvae found in dead or moribund plants might have died in the plant sometime after the harvest date. We did not test the continuing viability of the larvae beyond the harvest date.

It is possible that the differential response of the two insect species at the spring application over the 2 yr was caused, in part, by interspecific competition. When *A. zoegana* numbers were high (spring of 2003), *C. achates* numbers were low. Conversely, when *C. achates* numbers were high (spring of 2004), *A. zoegana* numbers were low. Because the insects normally coexist in high numbers in knapweed roots, competition does not seem to be an important factor in the normal maintenance of their populations. However, reduced vigor or mortality of the knapweed plants because of the herbicides may increase the impact of interspecific competition.

Of the two insect species, *A. zoegana* seemed to be more tolerant of the herbicide-caused knapweed mortality than *C. achates*. In 2003, an average of 0.7 ± 0.17 (SEM) *A. zoegana* larvae survived per plant in the plots sprayed in the fall of 2002, compared with 0.04 ± 0.04 for *C. achates*. Similarly, an average of 3.8 ± 0.66 *A. zoegana* larvae survived per plant in the plots sprayed in the spring of 2003 compared with 0.3 ± 0.20 for *C. achates*. Survival of *C. achates* in sprayed plants was higher in the spring spray plots in 2004 (4.8 ± 1.61 larvae/plant) but, as mentioned earlier, the survival was likely due solely to the reduced effectiveness of the herbicides in 2004. *A. zoegana*'s higher survival in the 2003 spring spray plots may be related to it's earlier development rate. Larval feeding cessation, pupation, and subsequent emergence of *A. zoegana* adults occur several weeks earlier than *C. achates* (Story et al. 1991, 1997), which may result in many *A. zoegana* larvae being unaffected by herbicide application at the spring rosette stage. Other factors possibly contributing to *A. zoegana's* greater survival in sprayed plants are feeding niche and greater tolerance for feeding on moribund plant tissue. As mentioned earlier, larvae of *A. zoegana* generally mine the outer tissues of the root while *C. achates* larvae mine the inner cortex tissue. Whether any of these factors could cause differences in insect survival is not known.

Based on our results, we concluded that fall application of these two herbicides is detrimental to both insect species and should be avoided if preservation of the insects is desired.

Based on the results of the 2003 experiment, when survival of *C. achates* larvae was equally low in both fall and spring applications, we might conclude that spring application of these two herbicides is not compatible with this agent. However, survival of *C. achates* larvae in 2004 was much higher after spring than after fall applications, which suggests that larval survival might improve if herbicide applications are delayed until a later plant growth stage. Application of these herbicides later in the spring (e.g., at the bolting stage) would probably have little or no effect on the insects because larvae of both species would have completed feeding and entered the pupal stage. However, 2,4-D is not effective when knapweed is in the bolting stage so there is no reason to apply it at this stage. Clopyralid, however, may be effective against knapweed at later growing stages (Pacific Northwest Weed Management Handbook 2004).

Additional studies are needed to assess the compatibility of the root insects with clopyralid and any other herbicides that can be effectively applied against spotted knapweed at the bolting and flowering stage. Once an application time is identified for clopyralid or other herbicides that is compatible with the two insect species, studies are needed to assess the minimum knapweed density necessary to maintain the insects. In addition to the temporal integration of herbicides and the biological control agents, studies are needed to assess the spatial integration of these methods, using unsprayed refugia for the biological control agents. The use of refugia could be particularly beneficial during fall applications, which were very detrimental to the insects.

Acknowledgments

We thank J. Corn and L. White for assistance. This report is based, in part, on research conducted and supported as a part of SAES Western Regional Research Project, W-1185.

References Cited

Duncan, C., J. Story, and R. Sheley. 2001. Montana knapweeds: identification, biology and management. Montana Cooperative Extension Service Circular No. 311, Bozeman, MT.

Groh, H. 1944. Canadian weed survey. Second annual report. Canada Department of Agriculture. Ottawa, ON.

Haag, K. H. 1986. Effects of herbicide application on mortality and dispersive behavior of the water hyacinth weevils, *Neochetina eichhorniae* and *Neochetina bruchi* (Coleoptara: Curculionidae) Environ. Entomol. 15: 1192–1198.

Jacobs, J. S., R. L. Sheley, and J. M. Story. 2000. Use of picloram to enhance establishment of *Cyphocleonus achates* (Coleoptera: Curculionidae). Environ. Entomol. 29: 349–354.

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. 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 Technol. 3: 627–631.

Lym, R. G., and R. B. Carlson. 1994. Effect of herbicide treatment on leafy spurge gall midge (*Spurgia esulae*) population. Weed Technol. 8: 285–288.

Lym, R. G., and J. A. Nelson. 2002. Integration of *Aphthona* spp., flea beetles and herbicides for leafy spurge (*Euphorbia esula*) control. Weed Sci. 50: 812–819.

Morrison, R. G., N. K. Lownds, and T. M. Sterling. 1995. Picloram uptake, translocation, and efficacy in relation to water status of Russian knapweed (*Acroptilon repens*). Weed Sci. 43: 34–39.

McCaffrey, J. P., and R. H. Callihan. 1988. Compatibility of picloram and 2,4-D with *Urophora affinis* and *U. quadrifasciata* (Diptera: Tephritidae) for spotted knapweed control. Environ. Entomol. 17: 785–788.

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 Res. 29: 103–111.

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. Can. Entomol. 120: 109–124.

Ochsmann, J. 2001. On the taxonomy of spotted knapweed (*Centaurea stoebe* L.). *In* L. Smith (ed.), Proceedings of the first international knapweed symposium of the twenty-first century. Coeur d'Alene, ID. USDA-ARS, Albany, CA. 33–41.

Pacific Northwest Weed Management Handbook. 2004. Extension and station communications. Oregon State University, Corvallis, OR.

Rees, N. E., and P. K. Fay. 1989. Survival of leafy spurge hawk moths (*Hyles euphorbiae*) when larvae are exposed to 2,4-D or picloram. Weed Technol. 3: 429–431.

SAS Institute 1999. SAS/STAT user's guide. Version 7–1. SAS Institute, Cary, NC.

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

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. J. Appl. Entomol. 117: 35–50.

Story, J. M., and G. L. Piper. 2001. Status of biological control efforts against spotted and diffuse knapweed. Proceedings of the first international knapweed symposium of the twenty-first century, March 15–16, 2001, Coeur d'Alene, Idaho. USDA-ARS, Albany, CA. 33–41.

Story, J. M., K. W. Boggs, and, W. R. Good. 1988. Optimal timing of 2,4_D applications for compatibility with *Urophora affinis* and *U. quadrifasciata* (Diptera: Tephritidae) for control of spotted knapweed. Environ. Entomol. 17: 911–914.

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

Story, J. M., L. J. White, and W. R. Good. 1996. Propagation of *Cyphocleonus achates* (Fahraeus) (Coleoptera: Curculionidae) for biological control of spotted knapweed: procedures and cost. Biol. Control. 7: 167–171.

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. Can. Entomol. 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. Biol. Control. 17: 182–190.

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

Trumble, J. T., and L. T. Kok. 1979. Compatibility of *Rhinocyllos conicus* Froelich and 2,4-D for musk thistle control. Environ. Entomol. 8: 421–422.

Trumble, J. T., and L. T. Kok. 1980a. Impact of 2,4-D on *Ceuthorhynchidius horridus* (Coleoptera: Curculionidae) and their compatibility for integrated control of *Carduus* thistles. Weed Res. 20: 73–75.

Trumble, J. T., and L. T. Kok. 1980b. Integration of a thistlehead weevil and herbicide for *Carduus* thistle control. Prot. Ecol. 2: 57–64.

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 for publication 3 March 2005; accepted 17 November 2005.