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Integrated Management of Scotch Broom (*Cytisus scoparius*) Using Biological Control

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Integrated weed management strategies (IWM) are being advocated and employed to control invasive plants species. In this study, we compared three management strategies (biological control alone [BC], BC with fire [BC + F], and BC with mowing [BC + M]) to determine if physical controls reduce seed production by Scotch broom and interfere with the action of the biological control agent—the Scotch broom seed weevil. We measured seed production and seed predation by the weevil at both pod and plant scale, and seed bank density over two field seasons. We found no difference in the number of seeds per pod among management strategies. However, combining management strategies (BC + M and BC + F) resulted in significant reductions in pods per plant, mature seeds per plant, and seed bank density relative to biological control alone. We did not find differences among management strategies in number of weevils per pod or proportion of seeds predated by the weevil at either pod or whole-plant scale. However, combining management strategies (BC + M and BC + F) resulted in a significant reduction in healthy mature seeds per plant relative to biological control alone. Although both integrated strategies outperformed biological control alone in reducing seed production and the seed bank, with no statistical difference between them, we propose that short-rotation prescribed fire could prove to be a more effective strategy for long-term management of Scotch broom due to its potential for slightly greater depletion of the seed bank.

Nomenclature: Scotch broom, *Cytisus scoparius* (L.) Link; Scotch broom seed weevil, *Exapion fuscirostre* Fabricius.

Key words: Integrated weed management (IWM), invasive species, prescribed fire, mechanical removal.

The pervasiveness of invasive nonnative plants has become a problem worldwide (Moran et al. 2005; Paynter et al. 2003; Pimentel et al. 2005; Rejmánek et al. 2005). Aside from the negative ecological impacts of invasive plants (Mason and French 2008; Rejmánek et al. 2005; Sharma et al. 2005), they have high economic costs. In the United States alone, nonnative plants invade approximately 700,000 ha (1,729,738 ac) of wildlands per year and cause an estimated $34 billion in damage and associated control costs annually (Pimentel et al. 2005).

Several management strategies are employed to control the spread of invasive plants, including biological (natural enemies), chemical (herbicides) and physical (e.g., fire and mowing) techniques, but there is a growing consensus that a more effective approach would be to combine all three strategies under an integrated weed management (IWM) program (DiTomaso et al. 2006b; Lym 2005; Moran et al. 2005; Vitelli and Pitt 2006; Witkowski and Garner 2008). However, despite calls for more widespread use of IWM to combat invasive plants, the number of studies that have investigated and documented the effectiveness of integrating biological control with other management strategies is sparse (Ainsworth 2003; Vitelli and Pitt 2006). Most research in support of IWM has come from studies combining biological control with herbicides (Boydston and Williams 2004; Collier et al. 2007; Henne et al. 2005; Lym 2005; Wilson et al. 2004), but few have investigated the combination of biological control with fire (Briese 1996; Fellows and Newton 1999; Le Maitre et al. 2008), mechanical control (Kluth et al. 2003; Tipping 1991), or with both fire and mechanical control (Paynter and Flanagan 2004b).

The invasive nature of woody legumes has been well-documented (Moran et al. 2004; Paynter et al. 2003; Richardson and Kluge 2008). One example is Scotch broom [*Cytisus scoparius* (L.) Link], a perennial shrub that is native to Europe and North Africa. Scotch broom has been introduced into several countries around the world, including the United States, Australia, and South Africa, where it has been declared a ''noxious weed'' (Syrett et al. 1999). In the United States, Scotch broom was first

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Management Implications

High fecundity and large seed banks have limited the success of biological control of Scotch broom in the United States. However, there is awareness among land managers that effective control of weeds requires the integration of biological control with other control techniques. For example, land managers at Fort Lewis in Washington have used repeated prescribed fire and mechanical removal since the late 1980s to manage Scotch broom. In this study we examined if the integration of physical controls with biological control by the Scotch broom seed weevil could reduce seed production by Scotch broom and interfere with the action of the biological control agent.

We measured the impact of three management strategies, biological control alone (BC), and combination of BC with either fire (BC + F) or mowing (BC + M), on seed production and seed bank size, and seed predation by the weevil at both the pod and plant scale. Combining management strategies (BC + M and BC + F) resulted in significant reductions in the number of pods per plant, mature seeds per plant, and seed bank density relative to biological control alone. Weevil seed predation rates were enhanced in BC + M and BC + F plots, compared to BC-alone plots, but these differences were not consistently statistically significant. However, there was a reduction in number of healthy mature seeds per plant in both BC + M and BC + F plots, compared to BC-alone plots. We found no differences between BC + M and BC + F plots for any of these variables. There also was no difference among management strategies in the number of weevils per pod. These results show that management of Scotch broom necessitates the integration of biological control with repeated applications of physical control methods. Although both integrated strategies outperformed BC alone in reducing seed production and the seed bank, short-rotation prescribed fire might be more effective than mowing for long-term management of Scotch broom due to its potential for slightly greater depletion of the seed bank.

introduced into California as an ornamental in the 1860s and later was used to prevent erosion and to stabilize dunes (Bossard 2000). The plant now is found throughout the Pacific Northwest and eastern United States (Coombs and Pitcairn 2004) and has been documented to reduce native plant species richness and cover (Parker et al. 1997; Srinivasan et al. 2007; Wearne and Morgan 2004) and to alter soil nutrient cycles and chemistry (Caldwell 2006; Haubensak and Parker 2004) in areas it invades.

The Fort Lewis Military Installation, in the state of Washington, is home to large infestations of Scotch broom. A significant portion of the military base covers native prairies which historically have depended on periodic fires for long-term persistence (Tveten 1996). Unfortunately, fire suppression and human-caused disturbance has facilitated the invasion and spread of Scotch broom on prairies and oak woodland areas of the base. Areas where fire has been suppressed on prairies have been converted into dense Scotch broom stands (Tveten 1996).

Management of Scotch broom at Fort Lewis includes the use of fire, mechanical, and biological control. Two Scotch broom biological control agents, the Scotch broom twig miner (*Leucoptera spartifoliella* Hübner) and the Scotch broom seed weevil (*Exapion fuscirostre* Fabricius), were introduced into California in the early 1960s by the U.S. Department of Agriculture (USDA) (Andres 1979). Both insects are found throughout much of Scotch broom's native range (Syrett et al. 1999). They also are present in Fort Lewis, but the weevil is more abundant, because the twig miner is heavily parasitized (Coombs and Pitcairn 2004). Many other Scotch broom natural enemies found in the United States are the result of adventive introductions (Syrett et al. 1999; Waloff 1966); this includes another seed feeder, the Scotch broom bruchid (*Bruchidius villosus* Fabricius). The bruchid was accidentally introduced into the eastern United States in the early 1990s, and intentionally introduced in Oregon and Washington in the late 1990s (Coombs et al. 2008).

Only one study in California has quantified the impact of the two biological control agents on Scotch broom and it found no effect of insect herbivory on plant growth (Bossard and Rejmánek 1994). Although Bossard and Rejmánek (1994) found that the weevil damaged 22 to 91% of seeds, this had no impact on the reproductive capacity of Scotch broom. Thus, the overall impact of these agents on Scotch broom populations has been limited (Coombs and Pitcairn 2004; Julien and Griffiths 1999). Prolific seed production by Scotch broom and its ability to form long-lived seed banks (Rees and Paynter 1997) suggest that seedling establishment of Scotch broom is limited by the number microsites for germination rather than seed production (Crawley 2000; Myers and Risley 2000). Under these conditions, the conventional view is that seed predators are unlikely to have an impact on Scotch broom abundance (Crawley 2000). However, opposing viewpoints exist that many plants species are actually both seed and microsite limited, and oscillate between the two in time and space (Eriksson and Ehrlén 1992). Maron and Gardner (2000) used simulation models to show that seed predators can significantly reduce future plant abundance even under the existence of a long-lived seed bank, and concluded that the key issue is not whether a plant is seed-limited, but the frequency in which recruitment is seed- or microsite-limited across time and space. Empirical studies examining the effect of herbivores on plants with persistent seed bank are few, but show that herbivores can decrease growth rates of plant populations (Maron and Crone 2006).

Fire has been the primary strategy used by land managers to remove Scotch broom at Fort Lewis. The prescribed fire program has been implemented since 1978 and burns approximately 3,000 ha of prairie and oak woodland on a 3- to 5-yr rotation (Tveten 1996). Compared to mechanical control, prescribed fire is more effective, with Scotch broom mortality rates as high as 90% (P. Dunn,

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personal communication). A short fire cycle also depletes the seed bank of Scotch broom, because it stimulates germination of dormant seeds (Bossard 1993). Mechanical control of Scotch broom includes pulling and cutting with various conventional tools. In large and open terrain grasslands, plants are cut with a tractor-pulled rotary mower. However, mowing is less effective compared to prescribed fire, as little mortality and pronounced resprouting result from this treatment (P. Dunn, personal communication).

The objective of this study was to examine if the combination of physical controls and biological control, based on seed predation by the Scotch broom seed weevil, reduce seed production by Scotch broom and interfere with the action of the biological control agent. To accomplish this, we investigated the impact of three management strategies, biological control alone (BC), and the combination of BC with either fire (BC + F) or mowing (BC + M), on seed production and seed bank size, and the abundance and seed predation effectiveness of the Scotch broom weevil. We addressed the following questions: (1) Which management strategy is most effective in reducing seed production (at pod and plant scales) and seed bank densities for Scotch broom, and (2) Does the integration of physical controls with biological control interfere with the abundance of the seed weevil per pod, and the level of seed predation at pod and plant scales?

Materials and Methods

Study Organisms. Scotch broom is common in disturbed pastures, shrubland, grasslands, open forests, and roadsides, but can also colonize undisturbed habitats, where it can dominate plant communities by forming dense stands (Bossard 2000). The plant can grow to 3 m (9.8 ft) in height, but it is more commonly 1.5 to 2 m (Parsons and Cuthbertson 2001). Plants can live up to 15 yr (Parnell 1966) and flower at 2 to 3 yr of age, with pods containing 3 to 12 seeds each (Bossard 2000). Individual plants can produce from 72 to 5,649 seeds in its native region and from 9,650 to 14,212 seeds in the introduced region (Rees and Paynter 1997). Seeds are released from pods by explosive dehiscence in the summer. A large portion of seeds are dormant and can survive for at least 5 yr in the soil (Bossard 2000). Large seed banks are common and range from 460 to 10,000 seeds m^{-2} (383 to 8,333 seeds yd^{-2}) in the native region and from 190 to 27, 000 seeds m^{-2} in the introduced region (Rees and Paynter 1997).

The Scotch broom seed weevil is univoltine and overwinters as an adult in crevices along the stems of Scotch broom and in the litter (Parnell 1966). Overwintered adults emerge early in the spring and feed on new terminal stem growth and floral buds; feeding on flowers is required for egg development (Parnell 1966). Females bore holes into pods with their rostrum to lay single eggs next to fully formed but still immature seeds. When eggs hatch, the neonate larvae bore directly into seeds. Development from the larval (three instars) to adult stage occurs inside individual seeds, but feeding on an adjacent seed also can occur (Sanz and Gurrea 1999). Adults emerge from pods in summer when they open explosively in the heat to disperse mature seeds. These adults do not mate initially, but feed on terminal twigs before summer aestivation.

The Scotch broom seed weevil is host to an ectoparasitoid (*Pteromalus sequester* Walker). This wasp is the dominant parasitoid attacking the weevil in Europe (Parnell 1964) and North America (Coombs and Pitcairn 2004). It overwinters as an adult and attacks the mature larval and pupal stages of the weevil (Parnell 1964). Parasitism rates of the weevil of up to 28% have been reported in Oregon (Andres and Coombs 1995). In 2005, samples of wasps collected from pods in Fort Lewis were sent to a USDA taxonomist for identification and were identified as *P. sequester*.

Study Plots. All study plots were located on prairie grasslands within Fort Lewis, a 34,874 ha military base, located 19 km (11.8 mi) southwest of Tacoma, Washington (Schmidt 1997). This region is characterized by a maritime climate (Franklin and Dyrness 1988). The average annual temperature is 11 C (51.8 F), ranging from 6.8 to 16.2 C. The warmest month of the year is August, with an average maximum temperature of 24.7 C; the coldest month is January with an average minimum temperature of 1.7 C. Winters are wet and summers relatively dry (Franklin and Dyrness 1988). Average annual precipitation (total mm) is 988 mm (38.9 in), with 75% occurring between October and March.

Experimental Design. Stands of Scotch broom representing three combinations of management strategies, biological control alone (BC), BC with fire (BC + F), and BC with mowing (BC + M), were monitored in 2006 and 2007. The BC-alone plots had never been treated with either prescribed fire or mowing. The three plots were located in old-growth Scotch broom stands in Training Area (TA) 7S, 22, and 6. The habitat was open canopy pine forest and stand size averaged 1 ha. The mowed and fire-treated plots had been treated every 4 to 5 yr, and satisfied three criteria: (1) a minimum plant age of 3 yr to ensure the presence of reproductive plants, (2) same physical control treatment had been applied at every rotation, and (3) similar dates at which the treatment had last been applied. The stands selected varied in size from 7 to 49 ha and all were located on flat prairie grasslands. The mowed plots were located on TA 7N, 15, and 14, and the first and last treatment had been applied in 1993 and 2002, respectively. The fire-treated plots were located on TA 6, 4, and 5, and were first and last burned in 1989 and 2001, respectively.

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All plots were exposed to ambient population levels of the Scotch broom seed weevil. Two plots per management strategy were sampled in 2006 and three were sampled in 2007. Sampling was conducted in all plots at three different scales: individual pods, whole plants, and the seed bank in the soil.

Pod Sampling. In 2006, pods were sampled weekly from a 15 by 15 m plot located in the center of a Scotch broom stand. The plot was subdivided into 15 grid units, each 3 by 5 m, with each grid containing at least nine reproductive plants. At each sample date, one plant that had not been sampled previously was haphazardly selected per grid unit and 15 pods were collected at random from each (total of 225 pods $plot^{-1}$ wk^{-1}). In 2007, the grid was reduced to 10 grid units of the same size, so that 10 plants wk^{-1} (total of 150 pods $plot^{-1}$ wk^{-1}) were sampled. Sampling each year commenced in late June when beetle oviposition was detected on young, green pods and stopped at the first sign of pod dehiscence in early August (total of six sample dates per year).

Pods were dissected under a microscope to count the number of underdeveloped (seeds either aborted or shriveled and smaller than fully developed seeds), healthy mature (full size and dark), and predated mature seeds; the number of Scotch broom seed weevil eggs, larvae, pupae, and adults; and the number of weevils parasitized by *P. sequester*. Pod data were used to calculate plot means for the total number of seeds per pod (underdeveloped plus predated and healthy mature), number of mature seeds per pod (predated plus healthy), proportion of mature seeds predated per pod, and number of weevils (all stages) per pod at each sample date each year. Means were calculated by averaging each measurement across pods per plant ($n = 15$), and then averaging across plants per plot ($n = 15$ in 2006, $n = 10$ in 2007). Parasitism rate was calculated for each plot for the last three sample dates using the following formula: total parasitized weevils/total susceptible weevils plus total parasitized weevils. Susceptible weevils included late instar larvae and pupae which only occurred during the last three sample dates coinciding with the time the parasitoid was active.

Statistical Analysis. A repeated measures ANOVA was used to analyze each measurement per pod (total seeds, mature seeds, proportion of mature seeds predated, and number of Scotch broom seed weevils) over the six sample dates, with management strategy as the main effect, and sample date (week and year) as the repeated measure. When analysis indicated the effect of management strategy depended on sample date, each sample date was examined separately to determine if there were significant differences among management strategies. A Holm's sequential Bonferroni adjustment was applied to assure an experiment-wise error rate of 0.05 and determine the significance of each test (total of six tests, one for each date) (Holm 1979). If a significant management strategy effect was found within each sample date, multiple paired comparisons were performed to separate management strategies. A two-way ANOVA was used to test for the effects of management strategy, year, and their interaction on parasitism rate. Because a significant interaction was found, the data for each year were analyzed separately using a one-way ANOVA. Predation and parasitism rate were arcsine square-root transformed, number of Scotch broom seed weevils per pod was $\log_{10}$ (x + 1)-transformed, total seeds per pod was $\log_{10}$-transformed, and mature seeds per pod was square-root (x + 0.5)–transformed to improve normality and homoscedasticity. All analyses were run in IBM® SPSS® version 16 (IBM Corporation, Armonk, NY 10504) (Norušis 2005).

Plant Sampling. Reproductive plants were collected on a single sample date in late July when pods were mature, but prior to pod dehiscence. Individuals were selected by setting up five transects, each 25 m in length. A random numbers table was used to generate six distances between 1 and 25 m for each transect, and the plant closest to each distance along the transect was cut at ground level (total of 30 plants $plot^{-1}$). Plant height (measured from where the plant was cut to the longest branch tip) and the number of pods was recorded for each plant. The number of pods per plant subsequently was used to estimate both the number of mature and healthy mature seeds per plant based on the mean mature seeds per pod and mean healthy mature seeds per pod, respectively, for the same sample date from pod sampling above; and the proportion of mature seeds predated per plant based on the corresponding mean proportion of mature seeds predated per pod.

Statistical Analysis. Plant height, number of pods, mature and healthy mature seeds per plant, and proportion of mature seeds predated per plant, were analyzed as plot means. A two-way ANCOVA (factors: management strategy and year) was first conducted to look at the influence of plant height as a covariate for the number of pods, mature and healthy mature seeds per plant, and the proportion of mature seeds predated per plant. Because the covariate was not statistically significant ($P < 0.05$) for any of the variables, it was excluded from the final analyses. A two-way ANOVA was then used to test for the effects of management strategy, year, and their interaction on plant height, and seed production and seed predation per plant. Pairwise comparisons between management treatments were made using Tukey HSD multiple comparison tests. Pod and seed measurements per plant were $\log_{10}$-transformed and proportion of mature seeds predated was arcsine square-root–transformed to improve normality and homoscedasticity. All analyses were run in IBM SPSS version 16 (Norušis 2005).

Seed Bank. Sampling was conducted prior to pod dehiscence to ensure that the seed bank was not overestimated by including the current year's seed crop. Sampling locations were selected using the same approach as for the plant sampling, so that 30 soil samples were collected from each plot on each sample date. Soil samples were collected using a soil corer (AMS Soil Core Sampler, Forestry Suppliers, Inc., Jackson, MS) measuring 2.5 cm (1 in) in diameter and 10 cm in depth. The litter layer and soil core were placed into separate Ziploc® bags for transporting to the laboratory. Samples were stored in a refrigerator at 4 C to keep seeds from germinating, and were later sieved to count healthy mature (no insect damage) seeds. The mean number of healthy mature seeds per core (seeds from litter layer plus soil layer) was converted to mean number of seeds m^{-2} for each plot.

Statistical Analysis. A two-way ANOVA was used to test for the effects of management strategy, year, and their interaction on seed bank density (mean seeds m^{-2}). Pairwise comparisons between management strategies were made using the Tukey HSD multiple comparison test. Data were square-root (x + 0.5)–transformed to meet assumptions of normality and variance, and analyzed using IBM SPSS version 16 (Norušis 2005).

Results and Discussion

Scotch Broom Seed Production. *Seed Production per Pod (Six Sample Dates).* There was no effect of management strategy or year on the total seeds per pod or number of mature seeds per pod (Table 1). Averaged across management strategies, total seeds per pod did vary significantly between sample dates, but there was no clear pattern over time (Figure 1b). Although the number of mature seeds per pod increased significantly over time for all treatments, there was also a significant sample date by management strategy interaction (Figure 1a; Table 1). The interaction was caused by the BC-alone pods containing slightly fewer mature seeds than the BC + M and BC + F pods during the early sample dates (one to three), but then notably more mature seeds per pod than the other treatments at later sample dates (four to six). However, differences among treatments were not statistically significant at any of the sample dates after applying the sequential Bonferroni correction.

Seed Production per Plant. For the single sample date when seed pods were mature but had not yet begun to dehisce, plant height was significantly different among management strategies ($F_{2,9}$ = 33.57, P < 0.001), but not between years ($F_{1,9}$ = 0.11, P = 0.75) with no significant interaction ($F_{2,9}$ = 0.48, P = 0.64). BC-alone plants were 1.8 times taller than BC + M plants (P < 0.001) and 1.5 times taller than BC + F plants (P < 0.001). However, there was no difference in height between BC + M and BC + F plants (P = 0.13).

Plant height was not a significant covariate in explaining the number of pods ($F_{1,8}$ = 2.12, P = 0.18) or mature seeds ($F_{1,8}$ = 0.51, P = 0.50) per plant among management strategies. There was a significant effect of management strategy on both the number of pods per plant ($F_{2,9}$ = 5.23, P = 0.03; Figure 2a) and number of mature seeds per plant ($F_{2,9}$ = 6.46, P = 0.02; Figure 2b). BC + M plants produced 71% fewer pods than BC-alone plants (P = 0.02). Although BC + F plants produced 55% fewer pods than BC plants, this difference was not statistically significant (P = 0.11). Similarly, BC + M and BC + F plants produced 79% (P = 0.02) and 69% (P = 0.045) fewer mature seeds than BC plants, respectively (Figure 2b). There was no difference in either the number of pods (P = 0.60) or number of mature seeds (P = 0.86) per plant between the BC + M and BC + F plots. There was a significant year effect on the number of pods per plant ($F_{1,9}$ = 6.05, P = 0.04), but not for mature seeds per plant ($F_{1,9}$ = 4.47, P = 0.06). Averaged across management strategies, pod production per plant was twice as high in 2007 compared to 2006. Also, the effects of management strategy were similar between years (i.e., no significant interaction) for both number of pods per plant ($F_{2,9}$ = 0.33, P = 0.97) and mature seeds per plant ($F_{2,9}$ = 0.15, P = 0.87).

These results show that the effect of management strategy on Scotch broom seed production depended on the scale at which seed productivity was measured: pod vs. plant. There were no differences in total number of seeds per pod or number of mature seeds per pod among management strategies, indicating that combining fire or mowing with biological control did not reduce seed production at the pod scale. In contrast, combining fire or mowing with biological control reduced seed production at the whole-plant level, because the number of pods and mature seeds per plant was significantly lower in both BC + M and BC + F plots, compared to BC-alone plots. Mowing appeared to be a more effective adjunct to biological control than fire in reducing seed production; it reduced the number of pods and thus mature seeds per plant to a slightly greater extent compared to biological control alone (Figure 2).

Differences in pod productivity per plant between the BC-alone and two integrated management strategies could be due to direct effects of repeated fire or mowing treatments on plant allocation to reproduction. Mowing and burning might have directly exhausted root reserves of surviving plants, and consequently, because resources have to be allocated between growth and reproduction (Bazzaz et al. 2000), regrowth of these plants supported fewer pods.

In addition, repeated mowing and burning might have had indirect effects on pod productivity through interference

Table 1. Statistical analyses to test for the effect of management strategy (biological control alone, and biological control combined with fire or mowing) and sample date (week and year) on seed production by Scotch broom and seed predation by the Scotch broom seed weevil. Treatment effects with $P \leq 0.05$ (repeated measures ANOVA) are in boldface type. Data were $\log_{10}$-transformed (total seeds per pod), square-root (x + 0.5)–transformed (mature seeds per pod), arcsine square-root–transformed (proportion of mature seeds predated per pod), and $\log_{10}$ (x + 1)-transformed (seed weevils per pod) for analysis.

	Total seeds per pod			Mature seeds per pod			Proportion of mature seeds predated per pod			Seed weevils per pod		
Source of variation	df	*F*	P	df	*F*	P	df	*F*	P	df	*F*	P
Management strategy (MS)	2	1.18	0.42	2	0.09	0.92	2	0.84	0.52	2	0.24	0.80
Error	3			3			3			3		
Week	4.68	5.67	**0.01**	5	86.93	**< 0.001**	4.45	11.78	**< 0.001**	5	9.21	**< 0.001**
Week·MS	9.36	1.47	0.25	10	5.05	**0.003**	8.90	0.46	0.87	10	2.72	**0.04**
Error (week)	14.04			15			13.34			15		
Year	1	1.45	0.32	1	0.20	0.69	1	0.34	0.60	1	0.04	0.86
Year*MS	2	0.02	0.98	2	0.49	0.66	2	9.70	**0.05**	2	4.48	0.13
Error (year)	3			3			3			3		
Week·year	5	1.87	0.16	5	0.44	0.81	5	3.10	**0.04**	5	2.63	0.07
Week·year·MS	10	1.73	0.16	10	0.59	0.80	10	1.63	0.19	10	0.66	0.75
Error (week·year·MS)	15			15			15			15		

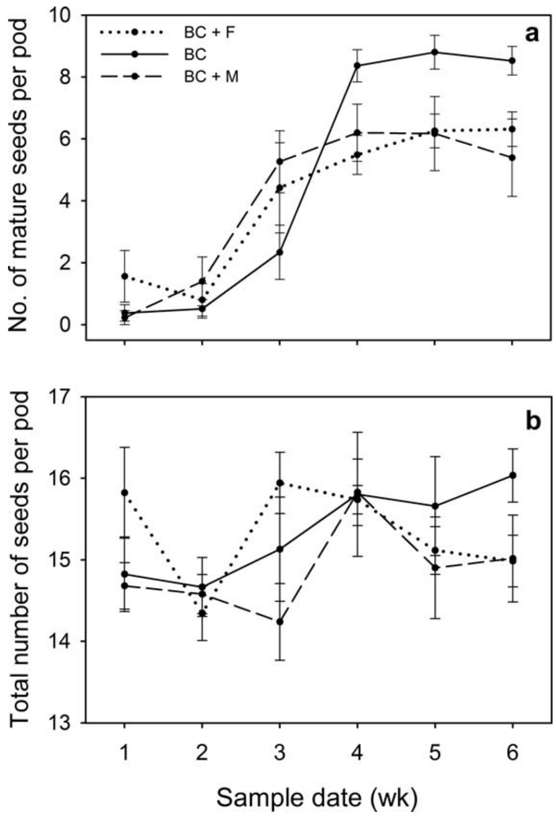

Figure 1. The mean (± 1 SE) number of mature seeds (a) and total seeds (b) per pod in relation to sample date in plots (n = 2 for 2006 and n = 3 for 2007) representing three Scotch broom management strategies: BC, biological control alone; BC + F, biological control combined with fire; and BC + M, biological control combined with mowing. Pods were sampled once a week from the last week of June through the first week of August (n = 6 wk).

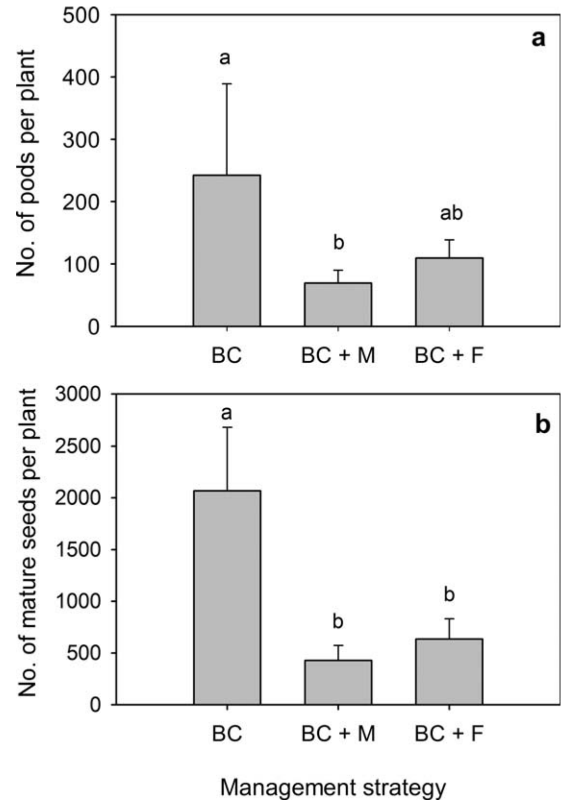

Figure 2. The mean (± 1 SE) number of pods (a) and mature seeds (b) per plant in plots (n = 2 for 2006 and n = 3 for 2007) representing three Scotch broom management strategies: BC, biological control alone; BC + F, biological control combined with fire; and BC + M, biological control combined with mowing. Plants were sampled on a single date in late July when pods were mature, but had not yet begun to dehisce. Columns not sharing the same letter are significantly different (ANOVA; $P < 0.05$).

with pollinators, because broom seed rain has been shown to be strongly correlated with pollinator visitation rates (Paynter et al. 2010), or through plant growth and density (Crawley 2000). Plants in the BC-alone plots were significantly taller than plants in the other two treatment plots, and several studies have shown plant height to be positively correlated with individual plant fecundity (Albert et al. 2008; Ollerton and Lack 1998; Sharma and Esler 2008; Witkowski and Garner 2008). However, our analysis did not show plant height to be a significant covariate in explaining differences in pod and seed production among management strategies. We hypothesize that the growth form and more compact structure of Scotch broom plants in the BC + M and BC + F plots might explain why these plants produced fewer pods. First, after being damaged by the physical controls, surviving plants lost their apical dominance (Aarssen 1995), resulting in shorter, multi-stemmed shrub-like individuals. In contrast, plants in the BC-alone plots were unistemmed, with a tree-like growth form. Second, treated plots contained a higher density of uniformly small (i.e., volume) plants in contrast to the low density, fewer large plants BC-alone plots. We did not measure plant density directly in this study, but trade-offs between plant density and individual fecundity have been documented elsewhere (Ågren et al. 2008; Bedane et al. 2009; Sheppard et al. 2002).

Differences in the age structure of plants among plots representing the three management strategies also could have influenced levels of pod production per plant (Crawley 2000; Rees and Paynter 1997). Plants from BC + M and BC + F plots were uniformly 4 and 5 yr old, respectively, whereas those from the old-growth BC-alone plots showed greater variability in age, and the reproductive plants were likely on average older and larger than those in the integrated management plots. Parnell (1966) showed that per unit biomass, 3 yr-old broom plants produced more pods than the 10- to 11-yr-old plants (pod production declines after plants are older than 10 yr and

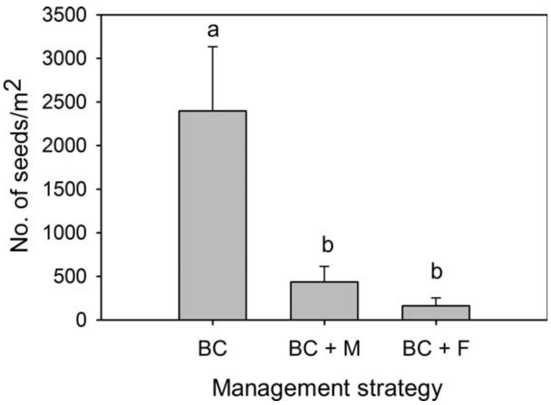

Figure 3. Mean (± 1 SE) healthy mature seed bank density in plots (n = 2 for 2006 and n = 3 for 2007) representing three Scotch broom management strategies: BC, biological control alone; BC + F, biological control combined with fire; and BC + M - biological control combined with mowing. Soil cores were sampled on a single date in late July when pods were mature, but had not yet begun to dehisce. Column not sharing the same letter are significantly different (ANOVA; $P < 0.05$).

begin to senesce), due to an increase in the ratio of wood to green growth as plants age (Waloff and Richards 1977). This suggests that plants from the BC + M and BC + F plots should have been at peak reproductive age compared to most of those in the BC-alone plots, yet they did not produce as many pods as BC-alone plants, indicating that plant age does not explain the observed differences in pod production per plant between the BC-alone and two integrated management strategies.

Scotch Broom Seed Bank. There was a significant effect of management strategy on healthy mature seed bank density m^{-2} ($F_{2,9} = 7.75$, $P = 0.01$), but not year ($F_{1,9} = 0.03$, $P = 0.88$). Also, the effects of management strategy were similar between years (interaction, $F_{2,9} = 0.01$, $P = 0.99$). The density of healthy mature seeds m^{-2} in BC-alone plots was significantly greater than in both BC + M ($P = 0.03$) and BC + F ($P = 0.01$) plots (Figure 3). There was no significant difference in the density of healthy mature seeds m^{-2} between BC + M and BC + F plots ($P = 0.79$).

Healthy mature seed bank density was significantly reduced when biological control was integrated with fire or mowing: by approximately 93% in the BC + F plots and by 82% in the BC + M plots compared to the BC-alone plots. The smaller seed banks in plots using the integrated management strategies result from a combination of reduced seed productivity and repeated disturbance events caused by fire and mowing. Disturbance has been shown to enhance Scotch broom seed germination (Downey and Smith 2000; Paynter et al. 1998), and fire disturbance can be particularly effective in depleting the seed bank because heat not only stimulates seed germination, but can also kill Scotch broom seeds directly (Bossard 1993). Significant depletion of the seed bank by repeated fire applications has been documented for both Scotch broom (Downey 2000) and for another closely related woody legume species, French broom [*Genista monspessulana* (L.) L.A.S Johnson] (Alexander and D'Antonio 2003; Odion and Haubensak 1997). Postdispersal seed predators also can influence seed bank densities, but are unlikely to explain our observed results because predation rates would have needed to be significantly higher in the disturbed integrated management plots than in the undisturbed BC-alone plots. Ants, mice, and birds have been observed to be predators of dispersed Scotch broom seeds in California (Bossard 1991), but to what degree these predators deplete the seed bank at Fort Lewis is unknown.

Seed Weevil Abundance and Seed Predation. *Seed Predation and Abundance per Pod.* The following results refer to seed predation by the Scotch broom seed weevil, as the Scotch broom bruchid was rarely observed in the pod dissections. There was no effect of management strategy on the proportion of mature seeds predated per pod (Figure 4a; Table 1). However, when averaged across sample dates within plots, the effect of management strategy on the proportion of mature seeds predated per pod varied by year (Figure 4b; Table 1). Seed predation per pod differed among management strategies in 2007 ($F_{2,6} = 9.11$, $P = 0.02$), but not 2006 ($F_{2,3} = 0.55$, $P = 0.63$). In 2007, seed predation in BC-alone pods (2%) was significantly lower compared to both BC + M (12%, $P = 0.02$) and BC + F (9%, $P = 0.04$) pods (Figure 4b). There was no difference in seed predation per pod between the BC + M and BC + F management strategies ($P = 0.72$). Additional data on number of healthy and predated mature seeds per pod for weevil-attacked pods is presented in Appendix A.

Averaged across management strategies, the proportion of mature seeds predated per pod increased significantly over time between sample dates (Figure 4a; Table 1). Also, a significant sample date by year interaction showed that, averaged across management strategies, the proportion of mature seeds predated per pod differed between years (Table 1). The interaction was due to lower seed predation per pod in 2007 than in 2006 during early sample dates (one to three), but higher than 2006 during later sample dates (four to six).

There was no effect of management strategy or year on the number Scotch broom seed weevils per pod (Table 1). The number of weevils per pod decreased significantly over time for all management strategies, but there was also a significant sample date (week) by management strategy interaction (Figure 5; Table 1). Although the number of weevils per pod was similar for both BC + M and BC + F pods throughout the sampling period, BC-alone pods

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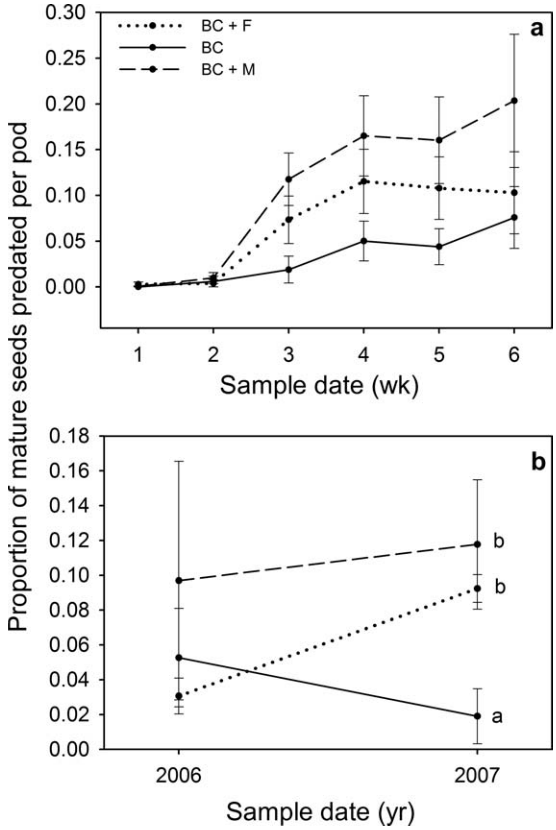

Figure 4. The mean (± 1 SE) proportion of mature seeds predated per pod by the Scotch broom seed weevil in relation to sample date by week (a) and year (b) in plots (n = 2 for 2006 and n = 3 for 2007) representing three Scotch broom management strategies: BC, biological control alone; BC + F, biological control combined with fire; and BC + M, biological control combined with mowing. Pods were sampled once a week from the last week of June through the first week of August (n = 6 wk). Means not sharing the same letter are significantly different (ANOVA; $P < 0.05$).

contained fewer weevils per pod at later sample dates (three to six). However, the differences among management strategies were not statistically significant at any of the sample dates.

For the last three sample dates combined, there was a significant interaction between management strategy and year for parasitism of the Scotch broom weevil by *P. sequester* ($F_{2,9}$ = 5.32, P = 0.03), with rates increasing from 2006 to 2007 for BC + F plots, but declining from 2006 to 2007 for the other two treatment plots (Figure 6). When the data were analyzed separately by year, there was no difference in parasitism rates among management strategies either in 2006 ($F_{2,3}$ = 8.14, P = 0.06) or 2007 ($F_{2,6}$ = 0.53, P = 0.61).

Seed Predation and Healthy Mature Seeds per Plant. Plant height was not a significant covariate in explaining the proportion of mature seeds predated ($F_{1,8}$ = 0.21, P = 0.66) or number of healthy mature seeds ($F_{1,8}$ = 0.46, P = 0.52) per plant among management strategies. There was no significant effect of management strategy ($F_{2,9}$ = 2.1, P = 0.18) on the proportion of mature seeds predated per plant, even though mean predation rates appeared to be higher in both BC + M and BC + F plots, compared to BC-alone plots (Figure 7a). There was a significant effect of management strategy on the number of healthy mature

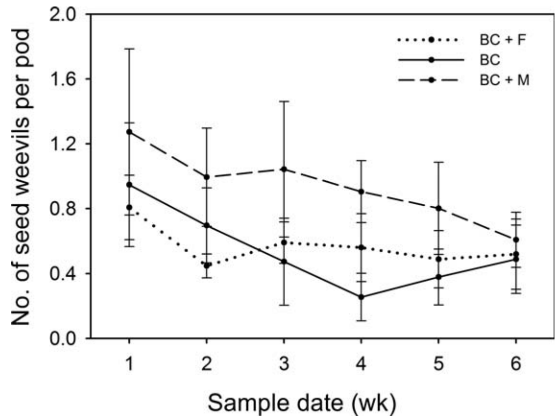

Figure 5. The mean (± 1 SE) number of Scotch broom seed weevils per pod (all stages) in relation to sample date in plots (n = 2 for 2006 and n = 3 for 2007) representing three Scotch broom management strategies: BC, biological control alone; BC + F, biological control combined with fire; abd BC + M, biological control combined with mowing. Pods were sampled once a week from the last week of June through the first week of August (n = 6 wk).

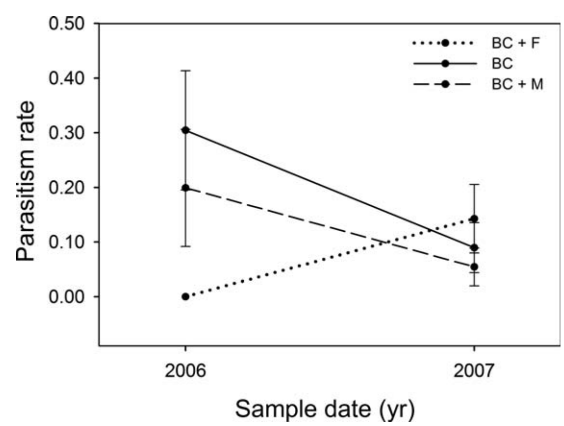

Figure 6. Mean (± 1 SE) parasitism rate of the Scotch broom seed weevil by *Pteromalus sequester* over two field seasons in plots (n = 2 for 2006 and n = 3 for 2007) representing three Scotch broom management strategies: BC, biological control alone; BC + F, biological control combined with fire; and BC + M, biological control combined with mowing. Pods were sampled once a week from mid-July through the first week of August (n = 3 wk).

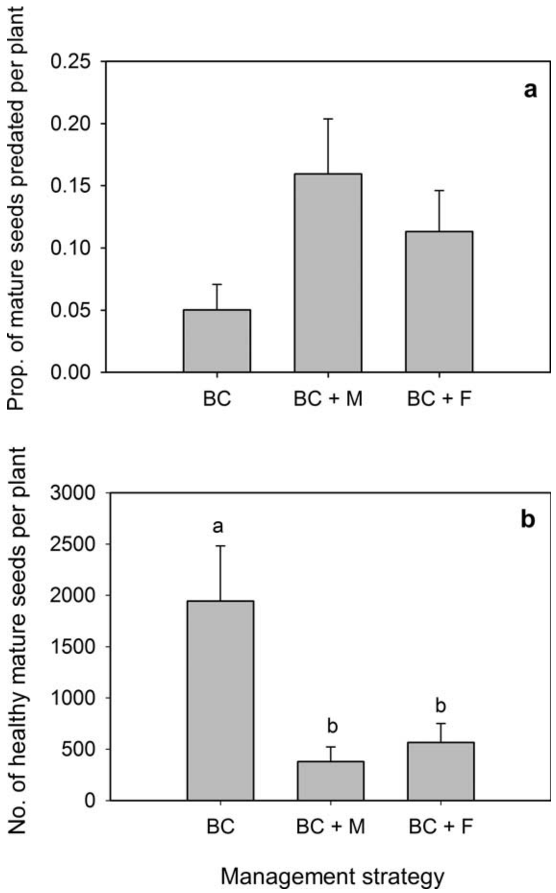

Figure 7. The mean (± 1 SE) proportion of mature seeds predated per plant by the Scotch broom seed weevil (a) and number of healthy mature seeds per plant (b) in plots (n = 2 for 2006 and n = 3 for 2007) representing three Scotch broom management strategies: BC, biological control alone; BC + F, biological control combined with fire; and BC + M, biological control combined with mowing. Plants were sampled on a single date in late July when pods were mature, but had not yet begun to dehisce.

seeds per plant ($F_{2,9}$ = 6.5, P = 0.02). BC + M and BC + F plants produced 81% (P = 0.02) and 71% (P = 0.045) fewer healthy mature seeds than BC-alone plants, respectively, but there was no difference in the number of healthy mature seeds per plant between BC + M and BC + F plots (P = 0.83; Figure 7b). There was no significant effect of year on both the proportion of mature seeds predated per plant ($F_{1,9}$ = 0.41, P = 0.54) and number of healthy mature seeds per plant ($F_{1,9}$ = 3.6, P = 0.09). There also was no significant interaction between management strategy and year for both proportion of mature seeds predated per plant ($F_{2,9}$ = 0.59, P = 0.58) and number of healthy mature seeds per plant ($F_{2,9}$ = 0.11, P = 0.90).

The Scotch broom seed weevil predated fewer than 21% of the mature seeds per pod and per plant (Figures 4 and 7a). These predation rates are relatively low, but within the range reported for other leguminous plant species targeted for biological control (Impson et al. 1999; 2004; Radford et al. 2001; Raghu et al. 2005; van Klinken 2005; van Klinken and Flack 2008). Moreover, seed predation by the Scotch broom seed weevil of less than 10% per plant has been reported for Scotch broom in its native region in Europe (Hosking 1992). However, the rate of seed predation observed in the current study was somewhat less than that observed in California by Bossard and Rejmánek (1994), who reported rates of 5 to 9% when mature pods first appear, rising to 22 to 91% by the end of the season. The later estimates reflect the spatial and temporal variation that often is associated with seed predation (Crawley 2000; Kolb et al. 2007).

Several studies have shown that plants with larger seed crops can suffer greater losses to seed predation (Ehrlén 1996; Jennersten and Nilsson 1993; Nurse et al. 2003; Sheppard et al. 1994). However, we found no consistent differences in the proportion of mature seeds that were predated by the Scotch broom seed weevil among the three management strategies at either the pod or whole plant scale (Figures 4 and 7a). Likewise, there was no effect of management strategy on weevil abundance per pod (Figure 5). Because BC-alone plants produced significantly more pods and mature seeds per plant than plants in the integrated management plots (Figure 2), these results suggest that the Scotch broom weevil was effective in responding to the greater abundance of pods in the BC-alone plots. However, the efficiency of seed predation in the BC-alone plots was not consistent among years (Table 1), being greater in 2006 than in 2007 (Figure 4b). This variation might be due in part to the greater production of pods per plant in 2007 than in 2006, but also could have resulted from a climatic influence on the synchronization of weevil adults and Scotch broom seed maturation.

For the Scotch broom seed weevil to have been effective in responding to the greater abundance of pods in the BC-alone plots in 2006 suggests that either individual females laid more eggs per plant in these plots than in the integrated management plots, or that a greater number of females accumulated per plant in the BC-alone plots. First, per-capita oviposition could increase with seed productivity if seed predators are time-limited and spend more time on plants with a greater numbers of pods. For example, oviposition of the Scotch broom seed weevil is closely tied to the production of flowers and pods by Scotch broom. Females need to feed on flowers in spring to initiate egg development (Parnell 1966), and then selectively lay eggs next to fully formed but still immature seeds within the pod (Sanz and Gurrea 1999). Thus, with a relatively short oviposition window, by spending more time per plant, female weevils might have been able to realize more of their oviposition potential in the BC-alone plots due to a greater abundance of pods (oviposition sites) at the right stage of development for attack by the weevil. In this regard, the duration of time spent by females of the specialist seed-feeding weevil (*Melanterius ventralis* Lea) on branches of its host, an invasive tree [*Acacia longifolia* (Andr.) Willd.], was found to be proportional to the number of pods on the branches and to the condition (seed maturity) of the pods (Donnelly and Hoffmann 2004). Second, plants producing more pods in the BC-alone plots could also have attracted a greater number of adult weevils. In general, it is considered that univoltine seed predators that show phenological synchrony with their host plant are well-equipped to track within-season peaks in resource availability (Raghu et al. 2005; van Klinken and Flack 2008; Westerman et al. 2003). Although we did not quantify the abundance of ovipositing Scotch broom seed weevils in the present study, other studies have shown that the abundance of seed predators can be positively correlated with the number of fruit produced per plant (Evans 1983; Sperens 1997).

Finally, mortality of immature seed predators due to parasitism can dampen the level of seed predation on leguminous plant species (Szentesi 2006; van Klinken and Flack 2008). However, we found no evidence of differential levels of parasitism of the Scotch broom seed weevil by *P. sequester* among management strategies, suggesting that integrated management strategies do not disrupt seed predation by the weevil through increased parasitism.

Management Implications for Scotch Broom. Both integrated management strategies (BC + M and BC + F) were more effective in reducing pod and seed production, and the seed bank density of Scotch broom than BC alone. Seed predation by the Scotch broom seed weevil also appeared to be greater in integrated management plots compare to BC-alone plots, but these differences were not consistently statistically significant (Figure 4). Nevertheless, results from this study provide additional support for the conclusion from other field studies (DiTomaso et al. 2006a; Paynter and Flanagan 2004a; Richardson and Kluge 2008) and spatial models (Odom et al. 2003; Ramula et al. 2008; Rees and Hill 2001) that in many cases, weed control can be improved by integrating other control strategies with biological control. Integration of biological and other controls also has been shown to improve the management of other invasive species (Collier et al. 2007; Henne et al. 2005; Lym 2005), including legumes (Hoffmann and Moran 1998; Impson et al. 2004; Paynter and Flanagan 2004b; Zimmermann et al. 2004).

Disturbance events that effectively deplete the seed bank can not only switch woody legumes from being microsite- to seed-limited for recruitment, but can also serve to enhance the impact of seed predators (Buckley et al. 2004; Kolb et al. 2007; Maron and Gardner 2000; Odom et al. 2003). Although we found no significant differences in seed production and seed bank densities of Scotch broom between the two integrated management strategies, prescribed fire appeared to reduce the seed bank slightly more than mowing (Figure 3). Because long-lived seed banks buffer woody legumes from the effects of seed predation, and seedling recruitment is believed to be microsite- rather than seed-limited (Andersen 1989; Myers and Risley 2000), the combination of biological control with 3-yr rotation fires, timed early enough in the season to kill plants before they can replenish the seed bank, could prove to be the more effective strategy for long-term management of Scotch broom at Fort Lewis. Furthermore, prescribed fire applications on a 3- to 5-yr rotation did not cause significant changes (percent cover, frequency, and species diversity) to native prairie plant species at Fort Lewis (Tveten 1996), and have been shown to be more effective than mowing at killing reproductive plants because vigorous resprouting occurs more frequently from mowed stumps (P. Dunn, personal communication).

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Appendix A. Mean (± SE) healthy and predated mature seeds per pod for those pods in which the Scotch broom seed weevil was present, estimated from pods collected during the last week of the sampling period only (first week of August).

	Treatment[a]		
Parameter	BC	BC + M	BC + F
Healthy mature seeds per pod			
2006	5.83 ± 0.67	5.63 ± 3.38	4.60 ± 0.17
2007	7.38 ± 1.11	3.39 ± 1.42	5.16 ± 0.30
Predated mature seeds per pod			
2006	2.68 ± 0.50	2.05 ± 0.24	0.67 ± 0.67
2007	2.07 ± 0.25	2.07 ± 0.34	2.03 ± 0.17

[a] Abbreviations: BC, biological control alone; BC + F, biological control combined with fire; and BC + M, biological control combined with mowing.

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