

Effects of Picloram Application on Community Dominants Vary With Initial Levels of Spotted Knapweed (*Centaurea stoebe*) Invasion

Yvette K. Ortega and Dean E. Pearson*

Broadleaf herbicides are commonly used to suppress exotic weeds with the intent of releasing native species from negative impacts of invasion. However, weed control measures can also have unintended consequences that should be considered along with intended effects. We conducted a controlled field experiment within bunchgrass communities of western Montana to examine if broadcast application of the broadleaf herbicide, picloram, may mitigate impacts of the exotic forb, spotted knapweed, on the dominant native grass, bluebunch wheatgrass, and forb, arrowleaf balsamroot. Local-scale relationships between native species and spotted knapweed cover served as a baseline for evaluating treatment effects at differing spotted knapweed invasion levels. To examine secondary invasion, we also measured treatment effects on the exotic grass, downy brome, relative to initial levels of spotted knapweed cover. Picloram application suppressed spotted knapweed cover by 70 to 80%. Treatment appeared to release cover and seed production of bluebunch wheatgrass, causing increases that varied positively with initial spotted knapweed cover. Bluebunch wheatgrass measures were elevated by as much as fourfold in treated vs. control plots, exceeding baseline levels in noninvaded plots. For arrowleaf balsamroot, negative effects of treatment prevailed, particularly where initial spotted knapweed cover was low. Arrowleaf balsamroot cover and fecundity variables were reduced by as much as 60% in treated vs. control plots, to levels typifying baseline conditions in highly invaded plots. In addition, treatment released downy brome, with cover increases from 2- to 20-fold. A controlled experiment selectively removing spotted knapweed showed similar release of downy brome. Our results show that picloram effects can depend on initial levels of weed invasion and may include substantial side effects, particularly when broadcast applications are used. Integrated approaches that include seeding of desirable species may be needed to enhance plant community resistance to secondary invaders and reinvasion by the target weed.

Nomenclature: Picloram; downy brome, *Bromus tectorum* L. BRTE; spotted knapweed, *Centaurea stoebe* L. CEST8; arrowleaf balsamroot, *Balsamorhiza sagittata* (Pursh) Nutt. BASA3; bluebunch wheatgrass, *Pseudoroegneria spicata* (Pursh) A. Löve PSSP6.

Key words: Cheatgrass, competitive release, exotic plants, invader impacts, nontarget effects, restoration, secondary invasion.

Exotic plant invasions are among the greatest threats to natural systems (Mack et al. 2000). In response, management of these systems is increasingly directed at suppressing target invaders under the common assumption that suppression will release desirable community components from the deleterious effects of invasion. Weed control tools

like broadleaf herbicides are frequently used to help restore native plant communities (Reever Morghan et al. 2003; Rice and Toney 1998; Rice et al. 1997; USDA Forest Service 2008). Yet the community-level effects of weed control measures are rarely evaluated (Smith et al. 2006), and we often know little about the invader impacts we hope to mitigate (Levine et al. 2003). Furthermore, weed control measures can have unintended, sometimes deleterious side effects. These side effects arise from limitations in the selectivity of weed control tools, which can result in direct harm to nontarget species (Pearson and Ortega 2009; Simberloff et al. 2005). Side effects can also arise through

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*First and second authors: Ecologist and Research Ecologist, Rocky Mountain Research Station, USDA Forest Service, 800 E. Beckwith Ave., Missoula, MT 59801. Corresponding author's E-mail: yortega@fs.fed.us

Interpretive Summary

A fall broadcast spraying of picloram effectively suppressed cover of spotted knapweed, setting the stage for release of native species from invader impacts. However, treatment effects were complex and depended on initial levels of spotted knapweed invasion. Treatment depressed the dominant native forb, arrowleaf balsamroot, particularly at low initial levels of spotted knapweed invasion where cover of this species was reduced to levels typically found at high levels of invasion. Nontarget effects on arrowleaf balsamroot extended to seed production and abundance of seedling stage plants, which could lead to population declines if prolonged. In contrast, treatment appeared to alleviate impacts of spotted knapweed invasion on the dominant native grass, bluebunch wheatgrass, in most cases, elevating both cover and seed production. Release effects on this native grass were maximized where spotted knapweed invasion levels were initially moderate. Treatment also released cover of the secondary invader, downy brome, which initially occurred at low levels and replaced spotted knapweed as the dominant species. Treatment effects on downy brome peaked at the highest initial level of spotted knapweed invasion, but were substantial at all levels. Secondary invasion of downy brome may be problematic since this species is difficult to control and can incur severe ecosystem impacts; e.g., by increasing fire frequencies. Treatment effects persisted through the third and final post-treatment year and would likely be enforced by repeated applications used to maintain spotted knapweed control. Due to treatment side effects, broadcast picloram applications alone may not mitigate overall impacts of invasion on native species or restore conditions found in noninvaded communities. More selective application methods would better focus suppression on target weeds and localize side effects. Additionally, integrated approaches including post-treatment seeding may be necessary to promote desirable species over problematic invaders.

more complex, indirect pathways, such as when suppression of the target invader releases a secondary invader, causing one weed to replace another (D'Antonio et al. 2004; Hobbs and Humphries 1995; Pearson and Ortega 2009; Seastedt et al. 2008). Therefore, it should not be assumed that target invader suppression will mitigate negative impacts of invasion or shift conditions closer to the pre-invasion state (D'Antonio et al. 2004; Seastedt et al. 2008; Smith et al. 2006).

One invader heavily targeted by weed control programs is spotted knapweed (*Centaurea stoebe* L.; = *C. maculosa* Lam.), an exotic perennial forb prevalent in western North America (Sheley et al. 2000). Spotted knapweed is known to reach high densities in grasslands and reduce native plant diversity and cover, but knowledge of its specific impacts on native taxa is limited (Ortega and Pearson 2005). Broadleaf herbicides such as picloram are widely applied to control exotic forbs such as spotted knapweed (DiTomaso 2000), often in an effort to mitigate deleterious effects of invasion and benefit native grassland communities (e.g., Pearson and Fletcher 2008; Rice and Toney 1998; Rice et al. 1997; USDA Forest Service 2008). Broadleaf herbicide application may increase abundance of native grasses,

presumably through release from target invader impacts, but may also suppress native forbs and increase abundance of invasive grasses such as downy brome (cheatgrass, *Bromus tectorum* L.; Endress et al. 2008; Reever Morghan et al. 2003; Rice and Toney 1998; Rice et al. 1997; Rinella et al. 2009; Tyser et al. 1998). Previous studies have documented such general patterns of plant community response to broadleaf herbicides. However, these works have not related herbicide effects to baseline impacts of target invaders or elucidated how initial levels of invasion may influence treatment outcomes, including the strength of release effects on native species and secondary invaders. Additionally, few studies have evaluated demographic effects of herbicide application on native taxa to inform long-term consequences (Crone et al. 2009).

We conducted a controlled field experiment within grassland communities of western Montana to examine if broadcast application of picloram may mitigate impacts of spotted knapweed on cover and fecundity of native species and influence secondary invasion of downy brome. We focused on dominant species from prominent native and exotic functional groups to allow detailed examination of taxa likely to respond differentially to broadleaf herbicide treatment and have large influence on system properties (Hillebrand et al. 2008; Smith and Knapp 2003). To consider a range of local-scale conditions within communities, sampling was conducted in plots scattered across multiple sites initially containing variable levels of spotted knapweed and low levels of secondary invaders. Correlations between native species variables and spotted knapweed cover were used to represent baseline declines associated with spotted knapweed invasion in the absence of treatment. After 2 yr of sampling, picloram was applied across a range of spotted knapweed invasion levels, and treatment effects on focal species were evaluated for 3 subsequent years. This approach allowed us to distinguish apparent release effects associated with target invader suppression from other treatment effects including nontarget impacts of picloram. We also used a removal experiment to isolate effects of spotted knapweed on focal species.

Materials and Methods

We studied intermountain bunchgrass communities (Mueggler and Stewart 1980) with scatterings of ponderosa pine [*Pinus ponderosa* P. and C. Lawson] and Douglas-fir [*Pseudotsuga menziesii* (Mirbel) Franco] located on the Lolo National Forest in western Montana. Study sites were steep southwest-facing slopes separated by > 0.7 km (0.4 mi) at elevations of 1,300 to 1,700 m (4,265 to 5,578 ft). Disturbance was limited primarily to natural sources (wildlife activity and erosion from snowmelt), and sites had no known history of herbicide spraying. The dominant

native species, as measured by canopy cover, were arrowleaf balsamroot [*Balsamorhiza sagittata* (Pursh) Nutt.; Asteraceae], a tap-rooted perennial forb, and bluebunch wheatgrass [*Pseudoroegneria spicata* (Pursh) A. Löve; Poaceae], a perennial bunchgrass; together, these species comprised approximately half of the total native species cover (Ortega and Pearson 2005). We chose eight primary sites that were as similar as possible in terms of topography and native vegetation type but at differing stages of spotted knapweed invasion: four “invaded” sites contained extensive patches of spotted knapweed intermixed with native vegetation, while four “native” sites had yet to be invaded, with spotted knapweed infestations in the vicinity but only trace levels on the site itself ($< 1\%$ mean canopy cover; Ortega and Pearson 2005). The annual grass, downy brome, was the most common secondary exotic species and occurred at low levels ($< 3\%$ mean canopy cover) at all sites at the onset of the study (Ortega and Pearson 2005).

To capture a range of local-scale conditions (i.e., relevant at the plant neighborhood scale), $n = 52$ permanently marked 0.5-m^2 plots were systematically distributed at 20-m intervals along four transects oriented perpendicular to the slope and 50 m apart at each of the eight primary sites. These plots were sampled prior to treatment, 2001 to 2002. In October 2002, through coordination with active weed management efforts (USDA Forest Service 2001), plots at four primary sites (two invaded and two native) were treated with the broadleaf herbicide picloram (TordonTM 22K), broadcast by helicopter at a rate of 0.28 kg ae/ha (0.25 lb/ac), the lowest rate recommended for spotted knapweed control (Dow AgroSciences 2001). A 90% nonionic surfactant designed to enhance spreading of the herbicide over plant surfaces was also applied at a rate of 0.023 L/ha (0.32 oz/ac). To minimize harm to native species, treatment was conducted in fall when native forbs were largely senescent but spotted knapweed was actively growing (Rice et al. 1997). Following previous studies, post-treatment sampling was continued for three growing seasons to encompass the typical period of picloram's persistence in soil (Rice and Toney 1998; Rice et al. 1997). During this period, we expanded sampling to four additional untreated sites (two invaded, two native) to broaden assessment of baseline relationships between native species and spotted knapweed invasion.

Within each plot, we estimated canopy cover of arrowleaf balsamroot, bluebunch wheatgrass, spotted knapweed, and downy brome to the nearest 1%. To ensure accuracy and consistency, we marked plot frames to denote 1% cover increments, and cover estimation was conducted by the same two-person team at all sites in each year. We sampled plots twice per growing season: early during the wet period (May to June) and late during the dry period (July to August), averaging the two values for analysis (Ortega and Pearson 2005). Cover values for

downy brome included trace levels ($< 1\%$ mean canopy cover) of Japanese brome (*Bromus japonicus* Thunb. ex Murr.; Ortega and Pearson 2005) because the two species were difficult to distinguish prior to flowering. Plots with $> 25\%$ shrub cover were excluded from analysis ($n = 33$ of 624 plots) to focus on grassland-dominated vegetation.

We considered several measures of fecundity for native species. During the early sampling period, we counted the number of arrowleaf balsamroot inflorescences on stems rooted within plots. We examined recruitment of arrowleaf balsamroot within plots by counting seedling stage plants, defined as those < 10 cm high with pubescent, undifferentiated leaves. To assess arrowleaf balsamroot seed production (herbicide effects only), we randomly selected 30 plants per site, enclosing one seedhead per plant in bridal veil to contain seeds until maturation. Seeds were tested for viability using a 0.1% solution of tetrazolium (2,3,5-triphenyl-tetrazolium chloride; Grabe 1970). We assessed bluebunch wheatgrass seed production during the late sampling period by counting the number of flowering stems rooted within each plot and estimating the mean number of spikelets per stem calculated from three randomly selected stems per plot. These values were multiplied to estimate number of spikelets per plot. To test whether spikelet counts were representative of seed production, we randomly collected flowering stems within additional systematically located plots ($n = 3$ stems/plot, $n = 48$ plots/site; 2001 to 2002). This subsample showed that numbers of spikelets and seeds per year were highly correlated ($r > 0.99$, $P < 0.001$), supporting use of spikelet counts as an index of total seed production.

We conducted a separate experiment to isolate effects of spotted knapweed removal on arrowleaf balsamroot and downy brome, as previous experiments have primarily considered spotted knapweed's effects on native bunchgrasses (e.g., Marler et al. 1999). In 2001, at each of two primary invaded sites, we established thirty 1-m-radius plots, each centered on a mature arrowleaf balsamroot plant within a patch of spotted knapweed. We constrained randomly selected locations to assure plots were > 10 m apart and > 5 m from transects. Following the protocol described above, we estimated cover of arrowleaf balsamroot, spotted knapweed, and downy brome, and counted arrowleaf balsamroot inflorescences and seedling stage plants in each plot. In half of the plots (randomly selected) per site, we then removed spotted knapweed by clipping stems and applying the contact herbicide glyphosate (RoundupTM) to the exposed base of the plant with a dropper. This killed the plant without disturbing the soil. Sampling was repeated in 2002, but discontinued after picloram was broadcast sprayed at one of the sites.

Statistical Analyses. We used mixed effects linear models for all analyses (SAS²: PROC MIXED). Because spotted

knapweed effects were hypothesized to operate at the local scale, we considered the plot as the main sample unit while including site as a model factor. Spatial covariance parameters testing for autocorrelation among plots within sites did not improve AIC scores, so these terms were not included in final models. For the specific analyses described below, we inspected scatterplots of residuals for dependent variables to assess assumptions of normality, linearity, and homoscedasticity (Tabachnick and Fidell 1989).

Using data from untreated plots at 12 sites (i.e., pretreatment data from the four treated sites and all data from the four control sites and four additional untreated sites), we quantified baseline relationships between native species variables and cover of spotted knapweed. The plot level response across years was treated as a repeated measure in models, and the interaction of spotted knapweed cover and year was included to test for consistency of relationships across the 5 yr. Data from plots at six native sites were included in the analysis to represent the variation in native species associated with communities not yet invaded by spotted knapweed. This approach improved estimation of the y -intercept, the level of each variable in plots with no spotted knapweed, so that this parameter accounted for the range of conditions found within noninvaded communities and not just a subset of plots at invaded sites. Therefore, significant deviation from the y -intercept in relation to increasing spotted knapweed cover was more likely to represent invader impacts than background differences in invasibility (Ortega and Pearson 2005). To depict baseline relationships between native species and spotted knapweed invasion in untreated communities, we output least squares (SAS²: PROC MIXED, LSMEANS statement) means for each response variable at discrete points over the range of spotted knapweed cover observed on the sites: 0% cover (“no invasion”), 20% cover (“moderate”), and 40% cover (“high”).

We used analysis of covariance to test for effects of herbicide treatment on native species as a function of pretreatment conditions in plots at the eight primary sites (Neter et al. 1990). We used this approach to explicitly examine whether initial invasion levels influenced treatment effects. Each post-treatment year was analyzed separately, and data from 2002 were used to represent pretreatment levels. The model for each native response variable included the pretreatment level of the variable, the main treatment effect (i.e., treated vs. control plots), and two related interaction terms that allowed treatment effects to vary with pretreatment conditions: (1) the treatment by pretreatment level interaction, which we refer to as the “general” effect, tested for variation in the treatment effect in relation to initial levels of the response variable; and (2) the treatment by pretreatment level by pretreatment spotted knapweed cover interaction, which we refer to as

the “release” effect, tested for variation in the treatment effect in relation to initial levels of spotted knapweed cover and the response variable. While the general effect tested for treatment effects unrelated to suppression of spotted knapweed, e.g., nontarget impacts of picloram, the release effect tested the expectation that spotted knapweed suppression should lead to increases in native variables positively correlated with initial cover of the invader. Treatment effects were primarily accounted for by interaction terms, so we did not report test statistics for the main effect except in one case where the term was statistically significant (for all other cases $P > 0.25$). To evaluate overall treatment effects at successive levels of spotted knapweed invasion, we obtained least squares means for treated and control plots over a range of pretreatment conditions defined by the baseline relationship between each native response variable and spotted knapweed cover (see above).

To test for effects of herbicide treatment on downy brome cover, we followed the approach outlined for native species with a few exceptions. The main treatment effect on downy brome cover was strong ($P < 0.02$) and did not vary across pretreatment levels of the variable ($P > 0.49$ for all interactions). We therefore removed pretreatment downy brome cover from treatment terms. The final model contained (1) the main treatment effect, testing for differences between treated and control plots independent of initial spotted knapweed levels; and (2) the treatment by pretreatment spotted knapweed cover interaction, testing for a “release” effect, or differences that varied with initial spotted knapweed cover. To illustrate overall treatment effects on downy brome, we output least squares means for treated and control plots at successive pretreatment levels of spotted knapweed cover, fixing pretreatment levels of downy brome cover at the mean value observed in 2002.

To test for effects of experimental spotted knapweed removal, we used analysis of covariance, evaluating the interaction of treatment and the pretreatment level of each variable; i.e., the change from pretreatment levels in removal vs. control plots. We do not report results for the main treatment effect since the term was not statistically significant ($P > 0.4$).

Results and Discussion

Baseline Relationships Between Native Species and Spotted Knapweed. Across the 5 yr of the study, mean cover of the dominant native forb, arrowleaf balsamroot, was $\geq 12.0\%$ in plots with no spotted knapweed and did not vary significantly among years ($P = 0.79$), while mean cover of the dominant native grass, bluebunch wheatgrass, varied from 3.0 to 5.6% among years ($P < 0.001$; Table 1). Thus, cover of arrowleaf balsamroot was consistently more than twice that of bluebunch wheatgrass,

Table 1. Effects of spotted knapweed, year, and the interaction of spotted knapweed and year on native species cover and fecundity measures, based on mixed model analysis of plot data from 12 sites in western Montana, 2001 to 2005.

	Spotted knapweed				Year		Spotted knapweed $\times$ Year	
	Intercept	Slope	F ^a	P	F ^b	P	F ^b	P
Arrowleaf balsamroot								
Cover (%)	13.09	-0.15	14.7	< 0.001	0.4	0.79	0.1	0.97
No. inflorescences	1.45	-0.02	17.6	< 0.001	7.9	< 0.001	1.6	0.17
No. seedlings	0.89	0.02	1.1	0.38	20.1	< 0.001	3.0	0.02
Bluebunch wheatgrass								
Cover (%)	3.61	-0.08	42.4	< 0.001	8.1	< 0.001	0.7	0.61
No. spikelets	95.09	-2.72	10.9	0.001	47.4	< 0.001	2.9	0.02

^aDegrees of freedom (df) = 1 and 570.

^bdf = 4 and 570.

reflecting the prominence of forbs in many native grasslands of the region (Mueggler and Stewart 1980; Ortega and Pearson 2005; Pokorny et al. 2004). For both species, fecundity measures were highly variable among years ($P < 0.001$; Table 1), reflecting variation in background environmental conditions.

Native species variables decreased as spotted knapweed cover increased in plots. For arrowleaf balsamroot, both cover and number of inflorescences were negatively correlated with spotted knapweed cover ($P < 0.001$), and relationships with spotted knapweed did not vary among years ($P \geq 0.17$; Table 1). Number of seedling stage arrowleaf balsamroot plants showed no overall relationship with spotted knapweed cover ($P = 0.38$), but had strong negative relationships with spotted knapweed cover in years with relatively high seedling densities (slope = -0.14 and -0.11 for 2001 and 2002) and weak positive relationships in remaining years (slope = 0.02 to 0.03 for 2003 to 2005; $P = 0.02$; Table 1). Bluebunch wheatgrass cover was negatively correlated with spotted knapweed cover ($P < 0.001$), and the relationship with spotted knapweed did not vary significantly among years ($P = 0.61$; Table 1). Number of bluebunch wheatgrass spikelets was also negatively correlated with spotted knapweed cover ($P < 0.001$), with more strongly negative relationships in years with high vs. low spikelet production (slope = -1.12 and -2.72 for 2001 and 2005, vs. -0.16 to -0.35 for 2002 to 2004; $P = 0.02$; Table 1). Negative relationships between native species variables and spotted knapweed cover were likely representative of invader impacts given the analytical technique used, which accounted for the range of conditions found in noninvaded communities (Ortega and Pearson 2005). This conclusion is also supported by

past studies documenting short-term competitive effects of spotted knapweed on native bunchgrasses (Callaway et al. 1999; Marler et al. 1999) and a native forb species (Lesica and Shelly 1996).

Effects of Herbicide Treatment. Consistent with previous studies (e.g., Rice et al. 1997), broadcast treatment with picloram was effective at suppressing spotted knapweed across post-treatment years ($F_{1,399-408} > 69.0$, $P < 0.001$), with mean annual cover in treated vs. control plots reduced by 70 to 80% in year three (Figure 1).

Effects of picloram application on native species were influenced by pretreatment conditions and varied across baseline levels of spotted knapweed invasion. Treatment negatively affected the forb, arrowleaf balsamroot, causing visible signs of injury including twisted stems and curled leaves. In all 3 post-treatment years, the general treatment effect accounted for declines in arrowleaf balsamroot cover that increased in magnitude with pretreatment levels of the variable ($P < 0.001$; Table 2). In post-treatment years two and three, this effect was countered by a release effect accounting for treatment related increases in arrowleaf balsamroot cover that varied positively with pretreatment spotted knapweed cover ($P < 0.001$; Table 2). The overall treatment effect was strongly negative in areas with no initial spotted knapweed invasion, where mean arrowleaf balsamroot cover in treated vs. control plots was reduced by > 40% to levels typically found at high levels of spotted knapweed invasion (Figure 1). Thus, treatment effects in noninvaded plots were substantial relative to baseline declines associated with increasing levels of invasion. At moderate and high levels of invasion, arrowleaf balsamroot cover was relatively insensitive to treatment and remained

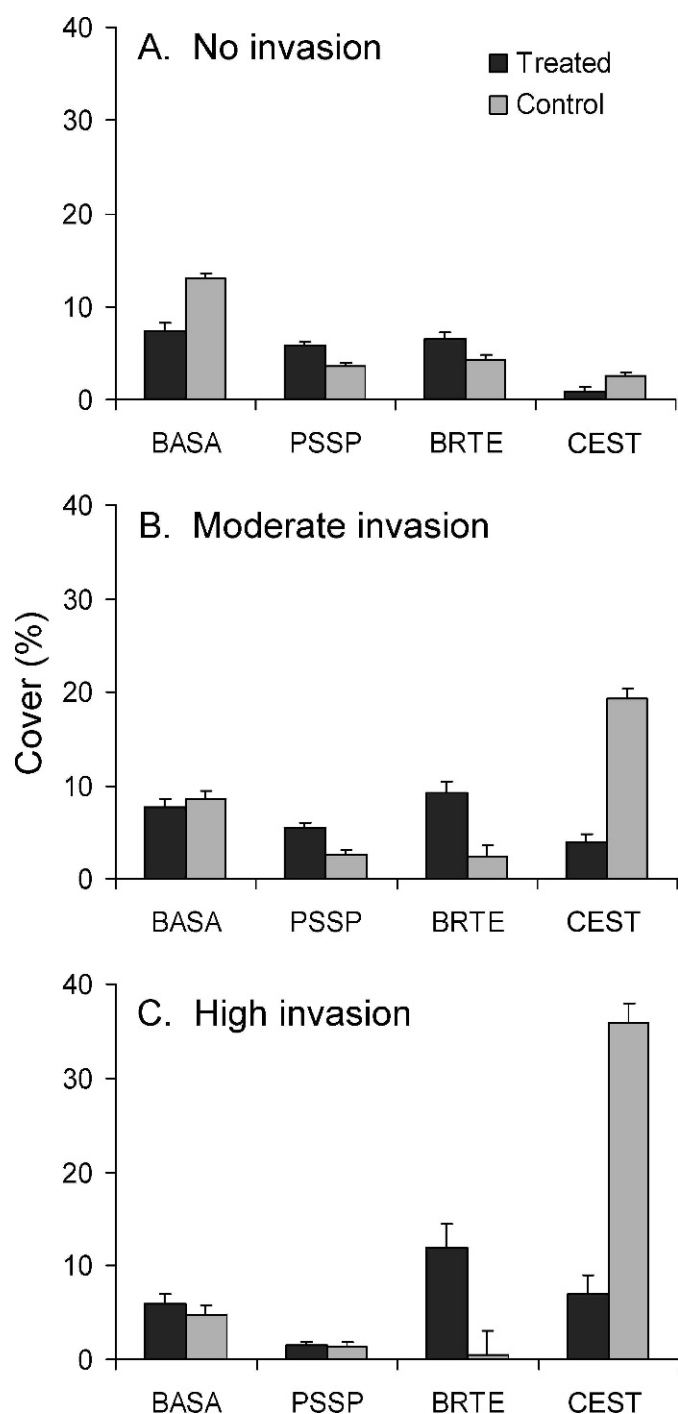


Figure 1. Effects of picloram application on cover of arrowleaf balsamroot (BASA), bluebunch wheatgrass (PSSP), downy brome (BRTE), and spotted knapweed (CEST) in the third year after spraying (2005), based on mixed model analysis of plot-level data from eight grassland sites in western Montana. Mean values $\pm$ Standard Error (SE) are given for treated and control plots at successive baseline levels of invasion defined by three pretreatment levels of spotted knapweed cover: (A) 0% ("no invasion"), (B) 20% ("moderate"), and (C) 40% ("high"), and corresponding pretreatment levels of each remaining species (see text).

depressed relative to levels found in control plots with no invasion (Figure 1).

Negative effects of spraying on arrowleaf balsamroot extended to fecundity measures. For inflorescence counts, the general treatment effect accounted for declines that increased in magnitude with pretreatment levels of the variable in post-treatment years one and two ($P < 0.001$) but not in year three ($P > 0.3$; Table 2). Picloram application also reduced numbers of seeds and viable seeds per seedhead, with effects persisting into year three ($F_{1,98-112} > 5.4$, $P < 0.03$). In addition, numbers of seedling stage arrowleaf balsamroot plants were reduced by treatment in all 3 post-treatment years, with general effects accounting for declines that varied positively with pretreatment levels of the variable ($P < 0.001$; Table 2). As a result, where spotted knapweed was initially absent, the mean number of seedling stage plants in treated vs. control plots was reduced by 50 to 60% across years to levels typically found in high invasion plots.

Picloram application positively affected the dominant native grass. In post-treatment years two and three, general treatment effects accounted for increases in bluebunch wheatgrass cover that varied positively with pretreatment levels of the variable ($P \leq 0.04$), while release effects accounted for increases that varied positively with initial spotted knapweed cover ($P \leq 0.01$; Table 2). Overall, bluebunch wheatgrass cover in treated vs. control plots increased by $> 50\%$ where spotted knapweed was initially absent, and $> 100\%$ where invasion levels were initially moderate, to reach mean cover values near 5% (Figure 1). Except at high invasion levels where bluebunch cover was sparse, treatment elevated cover of this species above levels typically found in no invasion plots to overcome baseline declines associated with spotted knapweed invasion (Figure 1).

Bluebunch wheatgrass seed production was also affected by picloram application. Release effects positively associated with pretreatment spotted knapweed cover contributed to treatment related increases in spikelet numbers in year two ($P < 0.001$) and year three ($P = 0.003$). Release effects were further bolstered by the main treatment effect (year two and three: $F_{1,394-403} > 5.2$, $P \leq 0.02$) and the general effect (year three only: $P = 0.04$; Table 2). Overall, treatment effects in these years produced mean spikelet levels in treatment plots that were more than double those in control plots, to exceed baseline levels found in plots without spotted knapweed invasion.

Picloram application had strong, positive effects on the exotic grass, downy brome. Mean cover of this secondary invader in untreated plots varied from a high of $3.7 \pm$ Standard Error (SE) of 0.67% in the year preceding herbicide treatment, to a low of $0.9 \pm 0.68\%$ in the first post-treatment year ($F_{3,576} = 19.6$, $P < 0.001$). The main treatment effect accounted for increases in downy brome

Table 2. Effects of picloram application on native species cover and fecundity measures in each of 3 yr following spraying (2003 to 2005), based on mixed model analysis of data from eight sites in western Montana. The difference between parameter estimates ($\Delta\beta$) is given for the general treatment effect (treatment by pretreatment level), measuring proportional change from pre- to post-treatment levels in treated vs. control plots independent of initial spotted knapweed cover; and the release effect (treatment by pretreatment level by pretreatment spotted knapweed cover), measuring proportional change from pre- to post-treatment levels per unit spotted knapweed cover in treated vs. control plots. Negative values indicate treatment related declines and positive values treatment related increases.

		General			Release		
	Year	$\Delta\beta$	F ^a	P	$\Delta\beta$	F ^b	P
Arrowleaf balsamroot							
Cover (%)	1	-0.67	163.5	< 0.001	< 0.01	1.2	0.29
	2	-0.50	49.8	< 0.001	0.02	12.4	< 0.001
	3	-0.52	54.0	< 0.001	0.02	5.9	0.003
No. inflorescences	1	-0.28	13.1	< 0.001	< -0.01	0.05	0.95
	2	-0.39	22.9	< 0.001	-0.04	14.5	< 0.001
	3	-0.05	0.8	0.38	-0.02	0.53	0.59
No. seedlings	1	-0.35	207.5	< 0.001	< 0.01	0.5	0.63
	2	-0.17	115.6	< 0.001	< -0.01	0.7	0.51
	3	-0.13	68.9	< 0.001	< -0.01	1.3	0.27
Bluebunch wheatgrass							
Cover (%)	1	0.08	1.3	0.25	0.02	1.5	0.22
	2	0.23	4.2	0.04	0.07	12.3	< 0.001
	3	0.37	10.9	0.001	0.04	4.7	0.01
No. spikelets	1	-0.08	4.0	< 0.05	< -0.01	1.2	0.31
	2	-0.18	0.3	0.61	0.08	7.3	< 0.001
	3	-0.65	4.8	0.03	0.11	5.8	0.003

^aDegrees of freedom (df) = 1, and 394 to 406.

^bdf = 2, and 394 to 406.

cover that were independent of pretreatment levels of downy brome and spotted knapweed cover in post-treatment year two ($P = 0.008$) and three ($P = 0.02$; Table 3). Thus, downy brome proliferated even in plots where it was initially absent, suggesting that low abundance of this invader at the site level was sufficient to allow widespread response to treatment. Similarly, treatment related increases in downy brome cover occurred even in plots where spotted knapweed was initially absent. Release effects that varied positively with initial spotted knapweed cover further contributed to increases in downy brome cover, particularly in year two ($P = 0.007$) and marginally so in years one ($P = 0.05$) and three ($P < 0.1$). Overall, picloram treatment resulted in elevated levels of downy brome (Figure 1). In most cases, mean downy brome cover increased by $> 100\%$ in treated vs. control plots. However, the response was even greater at high initial levels of spotted knapweed invasion, where mean downy brome cover increased by $> 2,000\%$ in treated vs. control plots to reach values close to 12%. Previous research has documented increases in exotic grasses following broadleaf herbicide treatments (Endress et al. 2008; Rice and Toney

1998; Sheley et al. 2006; Tyser et al. 1998), but only one study has related treatment effects to pretreatment levels of target weed invasion (Kedzie-Webb et al. 2002).

Spotted Knapweed Removal Experiment. Selective removal reduced spotted knapweed cover by 81%, as assessed 1 yr after the treatment (means for control and treatment = $22.3 \pm 1.0\%$ and $4.3 \pm 1.03\%$; $F_{1,55} = 16.8$, $P < 0.001$). Spotted knapweed removal increased numbers of seedling stage arrowleaf balsamroot plants by 65% (means for control and treatment = 7.7 ± 1.5 and 12.7 ± 1.59 seedlings; $F_{1,55} = 10.7$, $P = 0.002$), but did not significantly affect arrowleaf balsamroot cover ($F_{1,55} = 1.06$, $P = 0.31$) or inflorescence production ($F_{1,55} = 0.36$, $P = 0.55$). In our main herbicide experiment, release effects on arrowleaf balsamroot cover were not evident until the second post-treatment year, suggesting that our removal experiment was too short in duration to measure this effect. Conversely, increases in seedling stage plants were evident when spotted knapweed was removed selectively vs. with picloram, suggesting that nontarget effects of the herbicide counteracted benefits of spotted knapweed suppression.

Table 3. Effects of picloram application on cover of downy brome in each of 3 yr following spraying (2003 to 2005), based on mixed model analysis of data from eight sites in western Montana. The difference between parameter estimates ($\Delta\beta$) is given for the main treatment effect, measuring the difference in downy brome cover between treated and control plots independent of initial spotted knapweed cover; and the release effect (treatment by pretreatment spotted knapweed cover), measuring the difference per unit initial spotted knapweed cover. Negative values indicate treatment related declines and positive values treatment related increases.

Year	Main			Release		
	$\Delta\beta$	F ^a	P	$\Delta\beta$	F ^a	P
1	-0.69	1.46	0.23	0.07	2.9	0.05
2	1.51	7.2	0.008	0.23	5.1	0.007
3	2.61	5.4	0.02	0.23	2.4	0.09

^a Degrees of freedom (df) = 1, and 399 to 407.

Consistent with our picloram experiment, selective spotted knapweed removal doubled downy brome cover (means for control and treatment = $2.4 \pm 0.87\%$ and $5.5 \pm 0.88\%$; $F_{1,55} = 12.8$, $P < 0.001$).

Secondary invasion of exotic species has been documented following suppression of a variety of target weeds using a variety of control methods (see Pearson and Ortega 2009 for review). Suppression of the target invader may serve as a disturbance that increases availability of space or other resources, thereby facilitating secondary invasion of species resilient to control methods (Buckley et al. 2007). Secondary invasion of downy brome may be a particularly common consequence of weed control measures in western North America, given widespread occurrence of this species (DiTomaso 2000) and its ability to exploit resources released by suppression of perennial taxa (Chambers et al. 2007), outcompete native grasses (Vasquez et al. 2008), and attain dominance even when present at low initial densities (this study).

Overall, we found that broadcast spraying of picloram had complex local-scale effects. Apparent release effects associated with spotted knapweed suppression were significant for some native response variables. These release effects were influenced by the initial prevalence of the native species and the invader within study plots, peaking at moderate invasion levels and diminishing at low invasion levels (i.e., where spotted knapweed was sparse) and at high invasion levels (i.e., where native species were sparse). Although release effects appeared to drive increases in bluebunch wheatgrass, release effects on arrowleaf balsamroot were weak relative to negative nontarget effects of treatment. Release effects also contributed to proliferation of the secondary invader, downy brome. Increases in downy brome were not limited in magnitude by its initial prevalence (i.e., no treatment by pretreatment downy brome interaction), underscoring the ability of this exotic annual to take advantage of conditions created by target invader suppression. In contrast, treatment effects on native

perennial species depended on their initial prevalence, with the magnitude of these effects increasing with pretreatment levels of the response variable.

Treatment effects persisted through the third and final sampling year and resulted in major shifts in community components that varied in magnitude with the initial level of spotted knapweed invasion. By depressing arrowleaf balsamroot while favoring bluebunch wheatgrass, treatment tended to homogenize cover of dominant native species relative to their baseline levels. This shift was greatest in plots with no initial spotted knapweed invasion, where arrowleaf balsamroot was reduced to levels typical of high invasion plots and bluebunch wheatgrass was elevated above typical no-invasion levels. Prevalence of dominant native species also shifted in plots with moderate levels of initial invasion, where increases in bluebunch wheatgrass were maximized. However, downy brome responded more strongly to treatment than bluebunch wheatgrass and replaced spotted knapweed as the dominant species. Treatment related increases in downy brome were substantial at all levels of initial spotted knapweed invasion, but especially at the highest level.

Observed effects of treatment on community components are likely relevant beyond the short-term sampling period. In contrast to our results, a previous study found that negative effects of picloram application on cover of nontarget taxa subsided within 3 yr of spraying (Rice and Toney 1998). However, a recent study found that negative effects on prevalence of some native forbs were still evident 16 yr following picloram treatment (Rinella et al. 2009). Furthermore, effects of initial herbicide application may be sustained and possibly compounded by follow-up treatments. Because additional weed control measures must be applied within 3 to 5 yr following initial treatment to counter reinvasion, herbicides like picloram are often applied repeatedly (e.g., Rice et al. 1997; Sheley et al. 2000; Tyser et al. 1998; USDA Forest Service 2008). For perennial forbs like arrowleaf balsamroot, reductions in

seed production and recruitment indicated by our results could translate to population declines, particularly if prolonged by repeated treatments (Crone et al. 2009). Conversely, for perennial grasses like bluebunch wheatgrass, elevated levels of seed production could eventually translate to population increases (e.g., Freville and Silvertown 2005). Repeated applications could also continue to favor increases in downy brome over native grasses given this species' superior ability to exploit conditions created by treatment (references above).

Treatment induced shifts in prevalence of dominant species could influence system conditions; e.g., by affecting patterns of resource use within plant communities or availability of resources for consumers (Hillebrand et al. 2008; Smith and Knapp 2003). Broadleaf herbicide treatments may further affect system conditions if observed treatment effects extend beyond focal species, as suggested by previous studies documenting group level responses to broadleaf herbicides (e.g., Reeve Morghan et al. 2003; Tyser et al. 1998). For example, treatments may further simplify spotted knapweed invaded grasslands by depressing native forbs, which commonly contribute substantially more to diversity than native grasses (Ortega and Pearson 2005; Pokorny et al. 2004), thereby impacting community properties including resistance to invasion (Maron and Marler 2007), with rippling effects on higher trophic levels (Ortega et al. 2006).

System conditions may be further impacted if broadleaf herbicide treatments promote dominance of invasive grasses, which impact native grasses and are difficult to control (D'Antonio and Vitousek 1992). Downy brome may be particularly problematic since it can alter disturbance regimes by increasing fire risk and reducing fire return intervals, thereby creating conditions that favor its persistence over native species (Chambers et al. 2007). Downy brome invasion may also impact food chains since it represents a poor resource for herbivores relative to native species (DiTomaso 2000).

The herbicide treatment examined in our study is widely used (e.g., DiTomaso 2000; Pearson and Fletcher 2008; Rice and Toney 1998; Shepard et al. 2004; USDA Forest Service 2001, 2008). Although broadcast spraying is a cost-efficient means of suppressing invaders like spotted knapweed over large areas, it is insensitive to variability in local-scale conditions that appeared to influence treatment effects in our study. Where feasible, more selective application measures based on local-scale conditions may allow better control of management outcomes. For example, by spot spraying weed patches and leaving surrounding areas intact, treatment side effects may be greatly localized. Such an approach may be especially effective during follow-up treatments to minimize reinforcing side effects of initial application. In addition, side effects on some native forb taxa may be reduced by using

herbicides other than picloram, although this may also reduce target invader control (e.g., Endress et al. 2008). Notably, observed side effects of picloram on arrowleaf balsamroot were still apparent even though spraying was conducted in the fall when this species was senescent, suggesting that even late season applications may incur nontarget impacts when persistent herbicides like picloram are used. To improve understanding of nontarget effects, additional research is needed to examine the long-term response of native plant populations to different broadleaf herbicide treatments (Crone et al. 2009). At sites where downy brome is present, a more integrated approach may be needed to reduce secondary invasion. For example, sowing seeds of desirable species following herbicide application may help usurp resources from secondary invaders and resist reinvasion by the target weed (DiTomaso 2000; Endress et al. 2008; Sheley et al. 2006; Tyser et al. 1998). More knowledge of invader succession and how it is influenced by properties of native communities is needed to improve mitigation and restoration efforts.

Weed management in natural systems often focuses on suppressing target invaders while intending to release desirable community components from negative impacts of invasion. However, because natural systems are complex and weed control measures can have adverse side effects, target invader suppression may not produce the desired results. We found that a broadcast application of picloram appeared to provide partial relief from spotted knapweed's impacts by releasing the dominant native grass, but also incurred substantial side effects by depressing the dominant native forb and promoting a problematic secondary invader. Such side effects may be considered acceptable when management goals are narrowly focused; e.g., when treatments are used to enhance grass production in rangelands (Sheley et al. 2006) or within localized areas such as trailheads to mitigate the spread of invasive species into pristine areas (Tyser et al. 1998). However, our results suggest that broadcast treatments with picloram, when used alone, are unlikely to mitigate the overall impacts of weed invasion on native species or restore conditions to their pre-invasion state.

Sources of Materials

¹ R-11™ nonionic surfactant, Wilbur-Ellis Co., 345 California Street, 27th floor, San Francisco, CA 94104.

² SAS 2003, Version 9.1; SAS Institute, Inc., 100 SAS Campus Drive, Cary, NC 27513.

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