Weed Science, 52:172–177. 2004

Influence of spotted knapweed (*Centaurea maculosa*) management treatments on arbuscular mycorrhizae and soil aggregation

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Spotted knapweed is an invasive mycorrhizal weed prevalent in the Pacific Northwest of the United States. Little is known about the effects of spotted knapweed or its management methods on soil quality and soil structure. This study compared soils from spotted knapweed–infested areas with areas where spotted knapweed is being managed using several herbicides and mechanical treatments. We measured concentrations of glomalin, a glycoprotein produced by arbuscular mycorrhizal fungi (AMF), that is correlated with soil aggregate stability, AMF hyphal length, and percent water-stable aggregates (WSA) in soils from managed and unmanaged areas. Areas with high knapweed density (unmanaged areas) generally had lower glomalin concentrations and AMF hyphal lengths compared with areas receiving chemical and combined mechanical–chemical management treatments. Total glomalin was significantly negatively correlated with percent knapweed cover. However, WSA was high (70 to 80%) in soils from all management treatments and was not affected by knapweed cover. Our results suggest that spotted knapweed does not have negative effects on soil quality from our study site, likely because of the high aggregate stability of the soils in the area. However, *Centaurea maculosa* may have negative effects on soil quality in soils with lower aggregate stability.

Nomenclature: Spotted knapweed, *Centaurea maculosa* Lam. CENMA.

Key words: Herbicides, mechanical treatments, invasive weeds, picloram, clopyralid, 2,4-D.

Spotted knapweed is an invasive plant from Eurasia that has invaded much of the Pacific Northwest in the United States. As an aggressive weed, spotted knapweed competes with native vegetation, often reducing native plant populations and biodiversity (Tyser and Key 1988). Livestock and wildlife forage plants are reduced, and surface water runoff, soil erosion, and stream sediments increase in areas invaded by spotted knapweed (Jacobs and Sheley 1998; Lacey et al. 1989). The competitiveness of spotted knapweed is likely due to a combination of factors including prolific seed production, high seed viability, and the ability of seeds to germinate during fall and plants that overwinter as rosettes (Lacey et al. 1990; Tyser and Key 1988). The absence of natural enemies and the selective grazing of other desirable forage plants contribute to its success as a competitor (Lacey et al. 1990; Tyser and Key 1988).

Numerous methods have been developed to manage spotted knapweed, including the application of herbicides and mechanical methods such as handpulling and mowing. Use of herbicides is the primary method of weed control in most rangelands and they effectively control spotted knapweed (DiTomaso 2000; Rice et al. 1997). Mechanical methods such as mowing and handpulling can prevent seed production and reduce the carbohydrate reserves to the plant (DiTomaso 2000). However, little is known about how these management methods affect the soil environment, including arbuscular mycorrhizae and soil structure. In addition, few studies have examined spotted knapweed–soil relationships. Lacey et al. (1989) conducted a comparative field study and found increased water runoff and stream sediment yield in areas invaded by spotted knapweed compared with adjacent noninvaded areas.

Investigating spotted knapweed influences on soil properties using an experimental approach, using controlled conditions, and eliminating confounding factors can help elucidate the underlying mechanisms that explain changes in soil properties in knapweed-invaded soils. Soil structure mediates many biological and physical processes in the soil ecosystem, such as water filtration, soil aeration, biogeochemical cycling, and susceptibility to erosion (Elliott and Coleman 1988; Hartge and Stewart 1995; Jastrow and Miller 1997; Oades 1984). Because soil structure plays such an important role in ecosystem function, monitoring changes in soil structure is important.

This field study examined the relationships between spotted knapweed and management methods (mechanical, chemical, and combined mechanical–chemical treatments) for spotted knapweed, focusing on their effects on mycorrhizal parameters and soil structure. Although several weedy species, including those belonging to the Chenopodiaceae, Brassicaceae, Polygonaceae, and Amaranthaceae families, are considered to be nonmycorrhizal (Pendleton and Smith 1983), spotted knapweed populations in western Montana are heavily colonized by arbuscular mycorrhizal fungi (AMF) (Marler et al. 1999). AMF are among the most important soil biota for maintaining stable soil aggregation (Jastrow and Miller 1997). AMF also produce glomalin, a glycoprotein that is important in soil aggregation. Glomalin concentrations in soil aggregates are highly correlated with the percentage of water-stable aggregates (WSA) (Wright and Upa-

Table 1. Effect of management treatments for spotted knapweed on different glomalin fractions, AM hyphal length, and aggregate water stability (1 to 2 mm).

	EEG[a]		TG		AM hyphal length		% Water stable aggregates (1–2 mm)
	F[b]	P > *F*	*F*	P > *F*	*F*	P > *F*	
Total soil							
Treatments	3.32	0.01	2.14	0.05	2.01	0.07	χ^2 = 14.9, df = 12, P = 0.25[c]
Block	0.97	0.40	1.87	0.18	3.49	0.05	
	TG		IRTG		IREEG		
	F	P > *F*	*F*	P > *F*	*F*	P > *F*	EEG
1- to 2-mm aggregates							
Treatments	2.71	0.03	0.71	0.71	0.59	0.81	χ^2 = 3.66, df = 11, P = 0.98[a]
Block	5.79	0.01	5.32	0.02	1.34	0.29	

[a] Abbreviations: ANOVA, analysis of variance; EEG, easily extractable glomalin; TG, total glomalin; IREEG, immunoreactive easily extractable glomalin; and IRTG, immunoreactive total glomalin; AM, arbuscular mycorrhizal.
[b] *F* and P: ANOVA Source.
[c] Chi-squared nonparametric test performed.

dhyaya 1998), and glomalin has a relatively slow turnover rate in soil (Rillig et al. 2001). Differences in glomalin concentrations, AMF hyphal length, and percent WSA were measured in spotted knapweed–invaded and spotted knapweed–managed areas to investigate responses of soil structure to spotted knapweed invasion and management. Differences in these response variables among management methods (mechanical treatments vs. chemical treatments vs. combined mechanical–chemical treatments) also were investigated.

Materials and Methods

Field Experiment and Sampling

This research was conducted at the Lolo National Forest, in the Blue Mountain Recreation Area, near Missoula, Montana (46°45′00″N, 114°07′30″W). The site is a grassland area characterized as an upland range dominated by bluebunch wheatgrass (*Agropyron spicatum*), rough fescue (*Festuca scabrella*), and Idaho fescue (*Festuca idahoensis*) (Brown et al. 1999). The area has been invaded by spotted knapweed and occurs on a loam soil. The experiment consisted of applying different management methods for spotted knapweed in the field, with all treatments arranged in a randomized complete block design containing three blocks based on slope position ($n = 3$). Each block contained plots (6 × 9 m) to which the treatments were applied. The plots were treated with different management methods for spotted knapweed, including mechanical, chemical, and combined mechanical–chemical treatments. Untreated plots, where no management methods for spotted knapweed were applied, were established as experimental controls.

Chemical treatments included herbicide applications delivered in the spring or fall of 1997. Herbicides were applied using a CO_2-pressurized backpack sprayer equipped with a 3.1-m, six-nozzle spray boom, calibrated to deliver 150 L ha^{-1}.

Herbicide applications in this study included picloram at 0.28 kg ha^{-1} (spring 1997) and 0.14 kg ha^{-1} (fall 1997); and clopyralid plus 2,4-D at 0.21 plus 1.12 kg ha^{-1} (spring 1997) and 0.67 plus 1.12 kg ha^{-1} (fall 1997). Mechanical treatments were applied from 1997 to 2000. These treatments included mowing and handpulling. Mowing was performed using a standard push-mower. Two mowing treatments were applied: (1) mowing twice (early and late bud growth stage) in 1997 only and (2) mowing twice in 1997, 1998, 1999, and 2000. Three handpulling treatments were applied: (1) handpulling two times per year at 4-wk intervals in 1997, (2) handpulling two times per year in 1997 and 1998, and (3) handpulling two times per year in 1997, 1998, 1999, and 2000. Combination methods of both mechanical and chemical treatments included mowing during the late bud growth stage and picloram application (0.14 kg ha^{-1}) in the fall of 1997, mowing during the late bud growth stage and clopyralid plus 2,4-D application (0.67 kg plus 1.12 kg ha^{-1}) in the fall of 1997, and handpulling annually from 1997 to 2000 with picloram application (0.14 kg ha^{-1}) in the fall of 1997. Posttreatment spotted knapweed cover data were collected using the point-frame method (Brown et al. 1999).

On September 15, 2000, five soil cores (2 cm diameter) were extracted from each plot, physically combined in polyethylene bags, dried overnight in a drying oven at 80 C, and then stored at room temperature for 4 days until analysis.

Hyphal and Glomalin Measurements

Hyphae were extracted from soil samples (4 g) using an aqueous extraction and filtration method according to Rillig et al. (1999). AM hyphae were distinguished at ×200 magnification (Miller et al. 1995). Hyphal length was determined using the line intersect method as described by Jakobsen et al. (1992) and Tennant (1975).

Two detection methods are used to quantify glomalin: the Bradford protein assay, yielding the easily extractable glomalin (EEG) and the total glomalin (TG) fractions, and an enzyme-linked immunosorbent assay (ELISA) (using the monoclonal antibody developed against crushed spores of *Glomus intraradices*; Wright and Upadhyaya 1998), yielding the immunoreactive easily extractable glomalin (IREEG) and immunoreactive total glomalin (IRTG) fractions. These glomalin fractions are operationally defined based on their extractability–solubility and detections methods (much like other soil fractions, such as humic acids). Although the

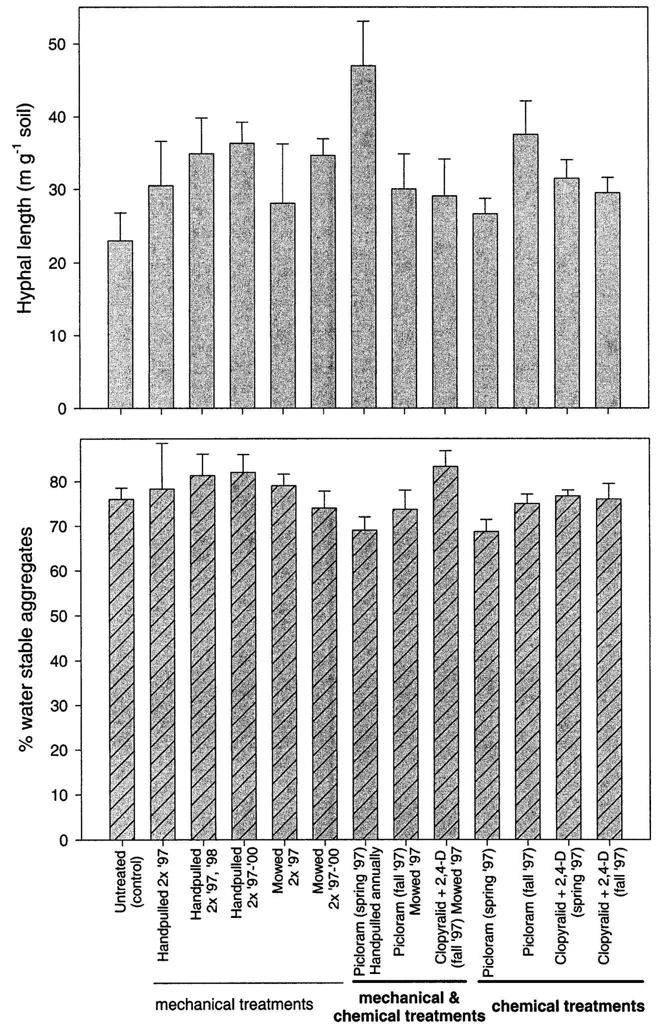

FIGURE 1. Arbuscular mycorrhizal hyphal length and aggregate water stability (1- to 2-mm soil aggregates) measured from soils treated with different management methods for spotted knapweed. Management methods that are indicated in bold (on x-axis) significantly lowered spotted knapweed cover. Standard errors are shown. Analysis of variance and chi-squared P values are presented in Table 1; contrast comparison P values are presented in Table 2.

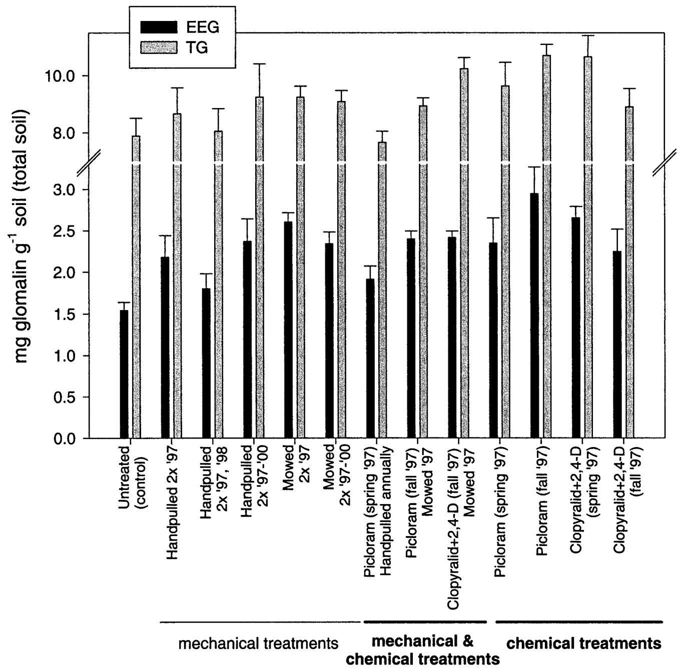

FIGURE 2. Concentrations of different glomalin fractions (total soil) measured from soils treated with different management methods for spotted knapweed. Management methods that are indicated in bold (on x-axis) significantly lowered spotted knapweed cover. Standard errors are shown. Analysis of variance P values are presented in Table 1; contrast comparison P values are presented in Table 2.

ELISA assay is a very specific detection method for glomalin, the more general Bradford protein assay also is used. This protein assay may capture glomalin protein that has undergone small (perhaps microbially mediated) changes, possibly resulting in the destruction or concealment of the epitope for the monoclonal antibody. Because of well-documented and strong correlations with aggregate stability (e.g., Wright and Upadhyaya 1998), the EEG and TG glomalin fractions measured by the Bradford assay continue to be quantified. Although the Bradford protein assay is generally used to measure total protein, it has been shown by sodium dodecyl sulfate-polyacrylamide gel electrophoresis that glomalin crude extract from soil (as measured by the Bradford assay) has banding patterns similar to those of glomalin extracts from single-species AMF sand cultures (Rillig et al. 2001).

Glomalin extractions from soil (1 g) were carried out as described by Wright and Upadhyaya (1996). Glomalin was extracted from total soil and also from 1- to 2-mm aggregates. The EEG fraction was extracted with 20 mM sodium citrate, pH 7.0 at 121 C for 30 min. After the EEG extraction, the TG fraction was extracted from the same 1 g of soil with 50 mM sodium citrate, pH 8.0 at 121 C for 60-min cycles until extraction was completed. Both fractions of glomalin were analyzed using the Bradford protein assay.[1] The glomalin fractions extracted from the 1- to 2-mm aggregates were further analyzed by ELISA, using the monoclonal antibody MAb32B11.[2] After all glomalin analyses were completed, two fractions of glomalin were obtained from total soil: EEG and TG. Four fractions of glomalin data were obtained from the 1- to 2-mm aggregates: EEG, TG, IREEG, and IRTG.

Soil Aggregate Water Stability ($WSA_{1–2\ mm}$)

The percentage of WSA in the 1-to 2-mm size class ($WSA_{1–2\ mm}$) was determined by a standard wet sieving method (Kemper and Rosenau 1986). The dried aggregates were then dispersed to determine coarse matter. The percentage of WSA for the 1- to 2-mm size class was calculated as the mass of aggregated soil remaining after wet sieving, correcting for coarse matter (> 0.25 mm).

Data Analysis

All response variables (glomalin concentrations, AM hyphal length, and $WSA_{1–2\ mm}$) were analyzed first using multivariate analysis of variance (MANOVA) using JMP (JMP version 3.1.6.2, 1996) because these variables cannot reasonably be assumed to be independent (Scheiner 1993). The response variables were then analyzed using analysis of variance (ANOVA; JMP version 3.1.6.2, 1996). Response variables that showed significant P values ($P \leq 0.05$) from the

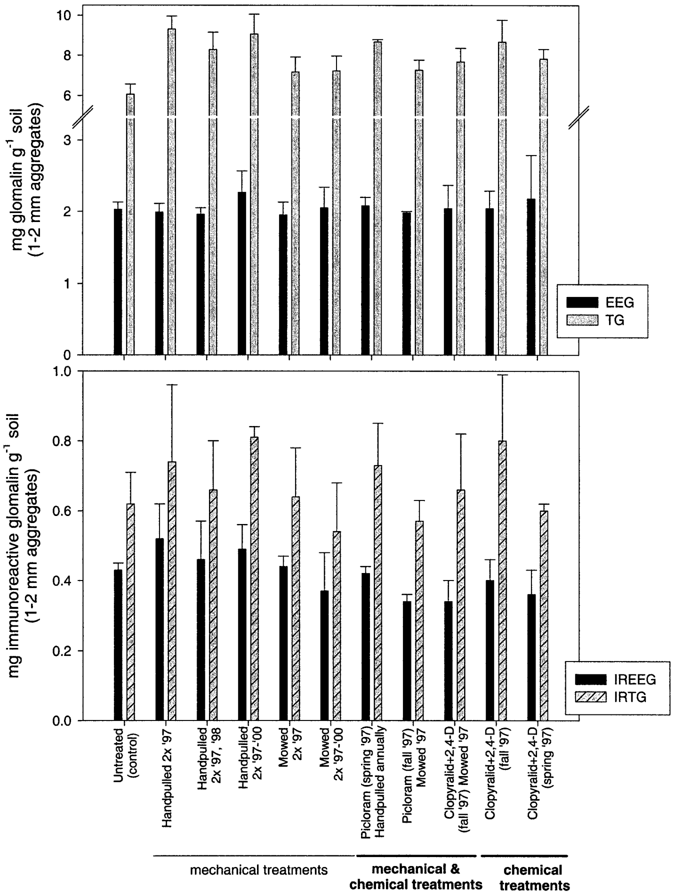

FIGURE 3. Concentrations of easily and immunoreactive extractable and total glomalin fractions (1- to 2-mm aggregates) measured from soils treated with different management methods for spotted knapweed. Management methods that are indicated in bold (on x-axis) significantly lowered spotted knapweed cover. Standard errors are shown. Analysis of variance P values are presented in Table 1; contrast comparison P values are presented in Table 2.

ANOVA analyses were analyzed further using linear contrasts (JMP version 3.1.6.2, 1996) to test for differences between untreated areas and managed areas and among the different management methods for spotted knapweed (mechanical vs. chemical vs. combined mechanical–chemical treatments). All data were normally distributed, as determined by the Shapiro–Wilks test (JMP version 3.1.6.2, 1996), except for percent WSA and EEG (1- to 2-mm aggregates). Data that were not normally distributed were log transformed and then analyzed. These data did not meet assumptions of the ANOVA analysis after transformation and therefore were analyzed with the chi-square nonparametric test (JMP version 3.1.6.2, 1996). Management methods that reduced spotted knapweed density compared with the untreated areas were determined by LSD analysis. Regressions between percent spotted knapweed cover and each response variable (total soil: EEG, TG, AM hyphal length, and $WSA_{1-2\ mm}$; 1- to 2-mm aggregates: EEG, TG, IREEG, and IRTG) were calculated using JMP (JMP version 3.1.6.2, 1996). Because of the low *n* values, we also discuss results with $P < 0.10$.

Results and Discussion

Two separate multivariate analyses were performed on two different data sets: the total soil data and the 1- to 2-mm aggregate data. Multivariate analysis of response variables measured on total soil (EEG, TG, AM hyphal length, and $WSA_{1-2\ mm}$) revealed a significant difference (MANOVA: $F_{14,24} = 2.20$, $P = 0.04$), justifying further analysis of individual response variables. Multivariate analysis of the 1- to 2-mm aggregate glomalin data set revealed marginally significant differences (EEG, TG, IREEG, and IRTG; MANOVA: $F_{13,16} = 2.28$, $P = 0.06$).

Differences among spotted knapweed management treatments were apparent in the total soil (Table 1). The total soil EEG and TG fractions both exhibited significant differences among treatments (Table 1). AM hyphal length was marginally significant ($P = 0.07$, Table 1); it was lower in the untreated plots than in plots receiving management treatments (Figure 1). $WSA_{1-2\ mm}$ was not significantly different among management treatments (Table 1). The aggregate water stability for the untreated plots as well as the treatment plots was high at 70 to 85%, with little variation between management treatments (Figure 1). Glomalin fractions analyzed from 1- to 2-mm-sized aggregates did not show a clear pattern among treatments. However, the TG

TABLE 2. Contrast comparisons of different management treatments for spotted knapweed from response variables with significant ANOVA P-values.

Contrast comparison			*F* ratio	*P* value
EEG (total soil)[a]	Untreated	All control methods	14.6	< 0.001
	Mechanical	Chemical	4.48	0.05
	Mechanical	Mechanical and chemical	0.01	0.92
	Chemical	Mechanical and chemical	3.82	0.06
TG (total soil)	Untreated	All control methods	3.83	0.06
	Mechanical	Chemical	6.20	0.02
	Mechanical	Mechanical and chemical	0.03	0.87
	Chemical	Mechanical and chemical	4.10	0.05
TG (1–2 mm)	Untreated	All control methods	11.2	< 0.005
	Mechanical	Chemical	0.03	0.87
	Mechanical	Mechanical and chemical	1.10	0.31
	Chemical	Mechanical and chemical	0.83	0.38
Hyphal length	Untreated	All control methods	5.09	0.03

[a] Abbreviations: ANOVA, analysis of variance; EEG, easily extractable glomalin; TG, total glomalin.

TABLE 3. Percent spotted knapweed cover in plots receiving different management treatments (average of three plots in each block).

LSD Treatment	Mean % cover	SE
Untreated (control)	54	1
Handpulled (three subtreatments combined)	47	9
Mowed (two subtreatments combined)	46	1
Picloram (spring 1997) and handpulled annually	1*	5
Picloram (fall 1997) and mowed (1997)	1*	0
Clopyralid + 2,4-D (spring 1997) and mowed (1997)	9*	4
Picloram (spring 1997)	0*	0
Picloram (fall 1997)	6*	3
Clopyralid + 2,4-D (spring 1997)	3*	1
Clopyralid + 2,4-D (fall 1997)	24*	7

* Indicates significant reduction in percent spotted knapweed cover compared with control ($P \leq 0.05$).

fraction did exhibit a significant difference among treatments (Table 1).

Response variables that showed a significant difference among different spotted knapweed management treatments were analyzed further by linear contrasts using JMP (JMP version 3.1.6.2, 1996). Management treatments were separated into groups on the basis of mechanical, chemical, or combined mechanical–chemical means, and contrast comparisons were performed between these groups of treatments for the response variables EEG (total soil), TG (total soil), TG (1 to 2 mm), and hyphal length. Untreated plots were significantly different from all management treatments for the EEG (total soil) fraction ($P < 0.001$), the TG (total soil) fraction ($P = 0.06$), the TG (1 to 2 mm) fraction ($P < 0.005$), and AM hyphal length ($P = 0.03$). Glomalin concentrations measured from total soil (Figure 2), 1- to 2-mm aggregates (Figure 3), and AM hyphal length (Figure 1) were lower in untreated plots compared with all management treatments. Significant differences ($P \leq 0.05$) occurred between the mechanical and chemical treatment methods as well as between the chemical and combined mechanical–chemical treatment methods in both the EEG and TG fractions (total soil) (Table 2).

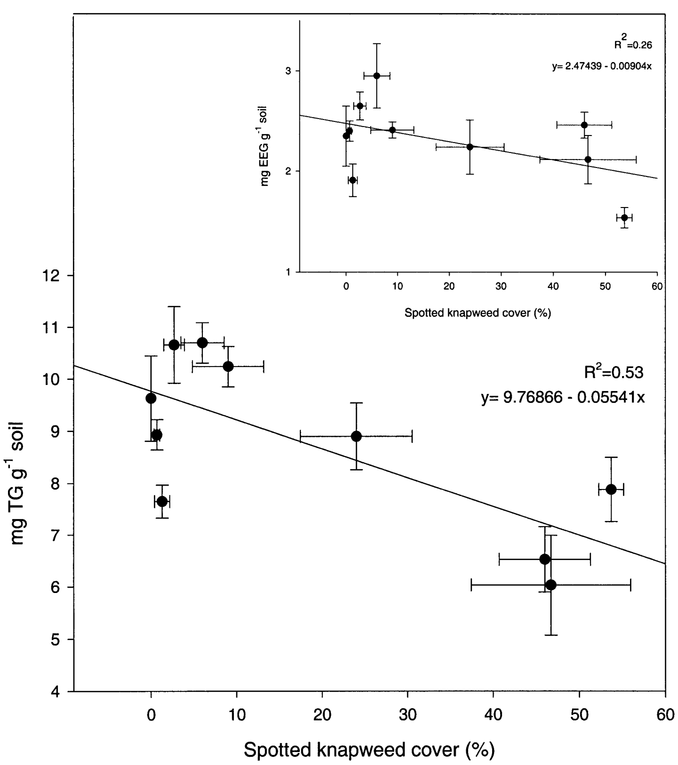

FIGURE 4. Regression of the concentration of TG (total soil) with percent spotted knapweed cover. R^2 value and linear equation are shown. Inset: regression of the concentration of easily extractable glomalin (total soil) with percent spotted knapweed cover. R^2 and linear equation are shown.

All management methods for spotted knapweed except the mechanical treatments were successful in reducing spotted knapweed cover compared with untreated areas ($P \leq 0.05$; Table 3).

Regression analysis showed that percent spotted knapweed cover had a significant negative linear correlation with total soil TG ($P \leq 0.05$; Figure 4), where there was a reduction in TG with increases in spotted knapweed cover. Total soil EEG showed a similar pattern but was not significant ($P = 0.13$; inset, Figure 4). Other response variables regressed with percent knapweed cover were not significant ($P < 0.05$).

Results indicate that the untreated areas had lower glomalin concentrations compared with areas that received management treatments. Because glomalin is highly correlated with soil aggregate water stability (Wright and Upadhyaya 1998), these results suggest that soil structure can deteriorate in areas where spotted knapweed infestations are not managed. Untreated, dense knapweed areas also had the lowest hyphal lengths compared with treated areas, further suggesting negative impacts of knapweed invasion. Mycorrhizal hyphae are often directly related to percent aggregate water stability (as they were in this study; $r = 0.98$). Hyphae entangle soil aggregates, assisting in soil aggregate formation (Jastrow and Miller 1997). Also, extracellular polymeric compounds on hyphal surfaces can sorb to inorganic materials, helping stabilize soil aggregates. Because hyphae help form and maintain soil aggregates, they are a key indicator of soil structure.

Soil aggregate water stability, a common measure of soil structure, did not show a pattern similar to that of glomalin concentrations and AM hyphal length. There were no significant differences in soil aggregate water stability between the untreated areas and those managed for spotted knapweed. The soil aggregate water stability in the soil measured was quite high (70 to 85%). The relationship of glomalin and soil aggregate water stability is curvilinear (Wright and Upadhyaya 1998), such that beyond a saturation point, a decrease in glomalin does not correlate with a major decrease in soil aggregate water stability. Thus, a decrease in soil aggregate water stability in untreated areas was not observed. However, spotted knapweed infestations occur in many areas in the Pacific Northwest where soil aggregate water stability is low. Our results suggest that spotted knapweed may exert a deleterious effect on soil structure in these areas.

Spotted knapweed cover (%) was significantly negatively correlated with the total soil TG fraction across all treatments, where TG decreased in areas with dense spotted knapweed. A similar, yet nonsignificant, linear relationship with the total soil EEG fraction was observed. This pattern further suggests that spotted knapweed has negative effects on soil parameters that are proportional to the density of the invasive weed.

This study has shown that spotted knapweed invasion has a negative effect on parameters associated with soil structure, as shown by a reduction in glomalin concentrations and hyphal length in untreated areas with a high density of this weed compared with managed areas with low spotted knapweed density. Overall, methods to manage spotted knapweed do not negatively affect soil structure compared with invaded, unmanaged areas. Chemical applications tend to result in higher concentrations of glomalin, suggesting that managing spotted knapweed with herbicides may be less deleterious to soil structure than mechanical or combined mechanical–chemical means. These findings offer information toward improving management practices for spotted knapweed, providing evidence that control methods for spotted knapweed are not deleterious to soil structure.

Sources of Materials

[1] Bradford protein assay, Bio-Rad Laboratories, Inc. 2000, Alfred Nobel Drive, Hercules, CA 94547.

[2] Monoclonal antibody MAb32B11, Dr. Sara Wright, Sustainable Agricultural Systems Laboratory, Beltsville, MD 20705.

Acknowledgments

The authors thank the USFS Lolo National Forest for providing the study site and Celestine Duncan and Dow AgroSciences LLC for establishment and maintenance of experimental plots. We also thank C. Duncan for valuable feedback and percent knapweed cover data. We thank Dr. Diana Six for valuable feedback. We thank Dr. Sara F. Wright for MAb32B11. Funding was provided by the Center for Invasive Plant Management, Montana State University.

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Received September 30, 2002, and approved September 15, 2003.