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RELATIONSHIPS BETWEEN *CENTAUREA MACULOSA* AND INDIGENOUS PLANT ASSEMBLAGES

Susan A. Kedzie-Webb[1], Roger L. Sheley[1], John J. Borkowski[2], and James S. Jacobs[1,3]

ABSTRACT.—Ecological impacts of invasive plants include displacement of indigenous species and declines in species richness and diversity. The objective of this study was to characterize the functional relationship between plant community composition and *Centaurea maculosa* Lam. (spotted knapweed) within a *Festuca idahoensis / Pseudoroegneria spicatum* habitat type in Montana. Density, cover, and biomass of all species were collected along a gradient of spotted knapweed cover ranging from 0% to about 100%. Step-down regression was used to determine the relationship among *C. maculosa*, indigenous species, species richness, and Shannon-Weaver's diversity index. Regressions showed that indigenous perennial grass cover, species richness, and species diversity were inversely related to *C. maculosa* cover. There was no relationship between *C. maculosa* and indigenous forbs. While this study does not imply a causal relationship, the literature suggests that *C. maculosa* displaces indigenous species and/or invades areas of reduced indigenous plant cover, low diversity, or low species richness. Knowing levels of indigenous perennial grass cover will help managers predict the outcome of weed management on rangelands that are vulnerable to weed infestation.

Key words: *spotted knapweed, noxious rangeland weeds, species richness, species diversity, invasive plants.*

Ecological impacts associated with non-indigenous weed invasions include displacement of indigenous species, degradation of ecosystem function, and declines in biodiversity (Vitousek 1986, Randall 1996). Invasive species can alter nutrient cycles, fire regimes, hydrologic cycles, and energy flow, and thus pose serious threats to ecosystem structure and function (Vitousek 1986, Vitousek et al. 1987, Vitousek and Walker 1989, Whisenant 1990). For example, *Bromus tectorum* L. (cheatgrass) is a winter annual that alters ecosystem processes. *Bromus tectorum* dominates millions of hectares in the Great Basin and has increased fire frequency from once every 60 to 110 years to once every 3 to 5 years (Mack 1981, Whisenant 1990). Indigenous shrubs of the Great Basin, which are not adapted to frequent fires, have been reduced in abundance or eliminated. Billings (1990) suggested that *B. tectorum* may reduce biotic and genetic diversity of *Artemisia*-dominated biomes by eliminating plant and animal species. This invasion has probably altered entire ecosystems. Like cheatgrass, *Centaurea maculosa* Lam. (spotted knapweed) is an important invasive plant in the Intermountain West. In a single, cursory study, *C. maculosa* increased erosion by 56% and sediment yield by 192% when compared with *Pseudoroegneria spicatum* (Pursh.) Löve–dominated rangeland under simulated rain events (Lacey et al. 1989).

Indigenous plant populations are thought to decline following invasion by nonindigenous weeds. For example, *Euphorbia esula* L. (leafy spurge) is a perennial weed that invades northern grasslands and displaces indigenous vegetation (Belcher and Wilson 1989). Similarly, Nuzzo (1993) reported that the cover of the indigenous ephemeral *Cardamina concatenata* (Michx.) Sw. (toothwort) declined from an average of 80% to 30% following invasion by the nonindigenous *Alliaria petiolata* (Bieb) Cavara and Grande (garlic mustard). Studies that address displacement of indigenous by nonindigenous species often allude to subsequent declines in biodiversity (Thompson et al. 1987, Webb and Kaunzinger 1993). However, few studies have quantified the functional relationship between indigenous plant assemblages and nonindigenous weed invasions.

The objective of this study was to characterize the functional relationship between plant community composition and *C. maculosa* within a *Festuca idahoensis / Pseudoroegneria spicatum* habitat type (Mueggler and Stewart 1980).

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We hypothesized that indigenous species cover, species richness, and species diversity are negatively related to *C. maculosa* cover. This hypothesis does not imply a causal relationship. Knowledge of these relationships is essential to predict plant community changes resulting from weed invasions.

METHODS

This study was conducted on 2 sites within a *Festuca idahoensis* / *Pseudoroegneria spicatum* habitat type (Mueggler and Stewart 1980) dominated by *F. idahoensis* with patchy infestations of *C. maculosa*. Site 1 is located in Story Hills (45°42′N, 111°01′W), 4 km northeast of Bozeman, Montana. Elevation at this site is 1478 m and average annual precipitation is 432 mm. Soils are clayey-skeletal, mixed Typic Argiborolls. Site 2 is located at Beartrap Canyon, about 45 km east of Norris, Montana (45°36′N, 111°34′W). Elevation at this site is 788 m with an average annual precipitation of 305 mm. Soils at site 2 are loamy-skeletal, mixed Aridic Argiborolls.

One *C. maculosa* patch, approximately 0.25 ha, was randomly selected at each site. We randomly located 5 transects, each 20 m long, within each patch. Transects radiated from dense *C. maculosa* in the center of each patch to an area of low or no *C. maculosa* occurrence on the outside of the patch. All transects radiated from the center of the same patch. The plant community at each transect origin was dominated by *C. maculosa* with few or no residual indigenous species in the understory. Transects ended in areas dominated by *F. idahoensis* with a diverse understory. Twenty permanent plots (20 × 50 cm, spacing between plots ranged from 0.5 to 2 m) were placed along each transect. *Centaurea maculosa* cover in the permanent plots ranged from 0% to nearly 100% (about every 5%). Density and cover of all species were sampled in each plot.

To avoid the effect of destructive sampling on permanent plots, we randomly selected 30 temporary plots (20 × 50 cm) along the *C. maculosa* gradient to sample biomass, seed bank, and soil nutrients at each site. We sampled biomass during August 1996 for all species by clipping plants to ground level. Clipped samples were dried at 60°C to a constant mass and weighed. The soil seed bank was sampled by extracting a soil core (65 mm deep and 80

mm in diameter) from each plot using a tulip bulb planter. Soil samples were dried at 60°C to constant mass and weighed. Two 100-cm^3 subsamples were taken from each sample, mixed, and sieved (0.5 mm) to separate seeds from soil and debris. Seeds were identified and counted. Additional 65 × 80-mm soil samples were collected from each plot to determine whether the *C. maculosa* gradient was related to differences in soil nutrients. Using a standardized extraction process (Page and Klute 1982), we tested soil samples for available nitrogen, phosphorus, and potassium. There were no differences in available soil nutrients; therefore, the data are not presented.

To test whether *C. maculosa* invasion was a function of seed availability only, we harvested 1 mature *C. maculosa* plant adjacent to each permanent plot (1 plant per plot), dissected it at root crown, and aged it by counting annual growth rings (Boggs and Story 1987). This procedure was used to test the assumption that invasion by *C. maculosa* is associated with availability of seeds rather than differences in soil and vegetation characteristics along the transects. Adult *C. maculosa* ranged in age from 1 to 7 years, but there were no differences in age and distance along transect. Therefore, data again are not presented.

Statistical Analysis

Data were compiled into tables showing number of transects (maximum of 5) along the *C. maculosa* gradient in which individual species were present for each site to characterize their presence and distribution. Plant density, cover, and biomass data were analyzed using a multi-step process. Covariance analysis was conducted to test for sample independence within transects. Because analysis indicated independence among all plots, we used a step-down linear regression procedure to identify the best model (Neter et al. 1985). A combination of *P*-value, model simplicity, and R^2 values was used to identify the best model for each step-down procedure. Scatter plots of residuals versus standardized predicted values were used to evaluate heterogeneity of variance for each model. Data transformations were conducted where necessary on predicted variables using square-root transformations. Inverse, quadratic, and log transformations were tested but did not improve the models. Colinearity was evaluated using a SAS tolerance

procedure to test for relatedness of predictors (SAS 1990). Colinearity was not a problem in this analysis. Linear regression models were fit using density, cover, and biomass of *F. idahoensis*, indigenous perennial grass, indigenous forbs, indigenous species richness, and indigenous species diversity as predicted variables. Regressor variables used were density, cover, and biomass of *C. maculosa.* For example, *C. maculosa* density, cover, and biomass were used to predict *F. idahoensis* density, cover, and biomass, respectively. Based upon the design of this observational study, regressions should not be interpreted to imply causality. Diversity was estimated using Shannon-Weaver's diversity index (Shannon and Weaver 1949). Means and standard deviations were calculated for soil seed bank samples.

RESULTS

Presence and Distribution

Eleven indigenous grasses (*P. spicatum, F. idahoensis, Pascopyrum smithii* [Rydberg] Löve, *Aristida purpurea* Nutt., *Bouteloua gracilis* [H.B.K.] Lag., *Danthonia unispicta* [Thurb.] Munro, *Koeleria macrantha* [Ledeb.], *Oryzopsis hymenoides* [R.&S.] Ricker, *Poa secunda* Presl, *Stipa comata* Trin. & Rupr., and *Stipa viridula* Trin.), 2 nonindigenous grasses (*Bromus japonicus* Thunb. and *Poa pratensis L.*), 12 indigenous forbs (*Achillea millefolium* L., *Artemisia ludoviciana* Nutt., *Aster falcatus* Lindl., *Antenarea* spp., *Balsamorhiza sagittata* [Pursh] Nutt., *Heterotheca villosa* [Pursh] Shinners, *Collomia linearis* Nutt., *Delphinium bicolor* Nutt., *Liatris punctata* Hook., *Linum lewisii* Pursh, *Lomatium dissectum* [Nutt.] Math. & Const., and *Lupinus* spp), and 3 nonindigenous forbs (*Alyssum alyssoides* L., *Comandra umbellata* [L.] Nutt., and *Tragopogon dubius* Scop.) were present at site 1. Of the indigenous grasses, *P. spicatum* was found in 2 or more transects along the gradient. All other indigenous grasses were limited in presence where *C. maculosa* cover was greater than 45%. Both nonindigenous grass species were present along the entire gradient. The most abundant indigenous forbs included *H. villosa* (hairy goldenaster) and *Lupinus* spp. The nonindigenous *A. alyssoides* was well represented along the gradient at site 1.

Eight indigenous grasses (*P. spicatum, F. idahoensis, B. gracilis, Calamovilfa longifolia* [Hook.] Scribn., *K. macrantha, Poa compressa* L., *P. secunda,* and *S. comata*), 2 nonindigenous grasses (*B. tectorum* and *P. pratensis*), 10 indigenous forbs (*Arabis holboellii* Hornem., *Artemisia frigida* Willd., *A. falcatus, B. sagittata, Coryphantha missouriensis* [Sweet] Britt. & Rose, *Gaillardia aristata* Pursh, *H. villosa, L. punctata, Lupinus* spp, and *Opuntia polyacantha* Haw.), and 3 nonindigenous forbs (*A. alyssoides, Berteroa incana* [L.] DC., and *T. dubius*) were present at site 2. *Pseudoroegneria spicatum* and *F. idahoensis* were present along most of the gradient. All other indigenous grasses were limited in presence where *C. maculosa* cover was greater than 50%. *Bromus tectorum* was present at all levels of *C. maculosa* cover and occurred in 3 or more transects, except at 70% and 100% cover, where it occurred in 2 and 1 transects, respectively. The most abundant indigenous forbs included *H. villosa* and *Lupinus* spp. Nonindigenous *A. alyssoides* and *B. incana* were well represented along the gradient at site 2.

Density

We generated general linear models to predict density of indigenous species (predicted variables) using *C. maculosa* density (regressor variable). For each increase in *C. maculosa* density (plants m^{-2}), perennial grasses decreased linearly by about 0.07 tillers m^{-2} at both sites (Fig. 1). *Festuca idahoensis* tiller density tended to decline rapidly as *C. maculosa* density approached 300 plants m^{-2}, and then continued to decrease, but less steeply at both
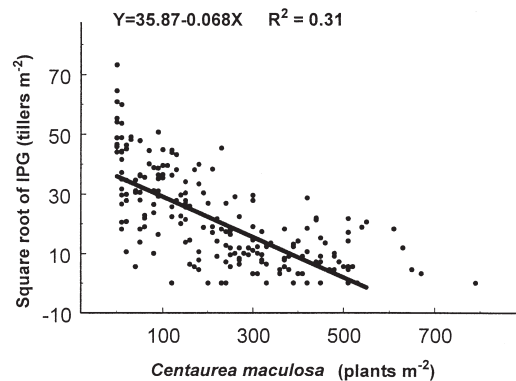

Fig. 1. Relationship between indigenous perennial grass (IPG) density and *C. maculosa* density. Sites were similar; regression models represent combined data.
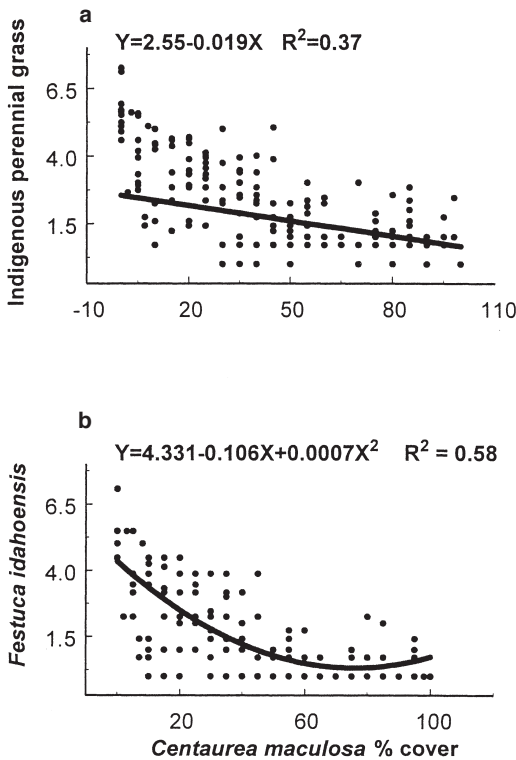
Fig. 2. Relationship between (a) indigenous perennial grass (IPG), (b) *F. idahoensis*, and *C. maculosa* cover. Sites were similar; regression models represent combined data.
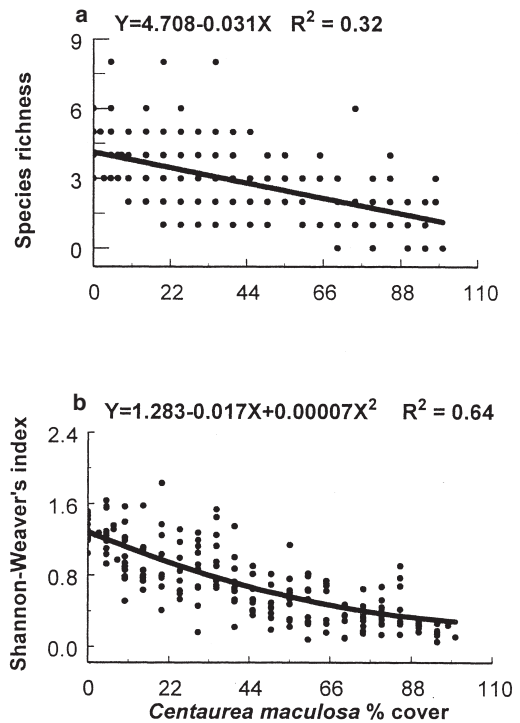

Fig. 3. Relationship between (a) species richness, (b) Shannon-Weaver's diversity index, and *C. maculosa* based on cover. Sites were similar; regression models represent combined data.

sites ($R^2 = 0.55$). Indigenous forb density was not associated with *C. maculosa* density at either site ($P \geq 0.1$).

Indigenous species richness was negatively related to *C. maculosa* density (plants m^{-2}) at site 2 ($R^2 = 0.39$). At site 1 species richness tended to decline until *C. maculosa* densities reached about 350 plants m^{-2}. Species diversity tended to increase slightly from about 1 to 2 Shannon-Weaver's diversity index units based on *C. maculosa* density, and then began to decrease after reaching approximately 400 plants m^{-2} ($R^2 = 0.30$).

Cover

General linear models indicated a negative relationship between indigenous grass cover and *C. maculosa* cover at both sites. For each 1% increase in *C. maculosa* cover, indigenous perennial grass cover decreased by about 2% (Fig. 2a). However, *F. idahoensis* cover declined with increasing *C. maculosa* cover until about 75% *C. maculosa*, after which this grass slight-

ly increased (Fig. 2b). Indigenous forb cover was not associated with *C. maculosa* cover (data not shown).

A negative relationship between indigenous species richness and *C. maculosa* cover was quantified at both sites. For each 1% increase in *C. maculosa* cover, species richness decreased by about 3% (Fig. 3a). At both sites the prediction of plant diversity resulted in a quadratic model with a *C. maculosa* × *C. maculosa* interaction (Fig. 3b). However, the quadratic component was so small that plant species diversity decreased nearly linearly based on *C. maculosa* cover.

Biomass

Indigenous perennial grass biomass was negatively related to *C. maculosa* biomass at both sites (Fig. 4a). Indigenous perennial grass biomass tended to decline quickly as *C. maculosa* biomass increased from 0 to 800 g m^{-2}, after which no further decrease in grass occurred. *Festuca idahoensis* biomass followed
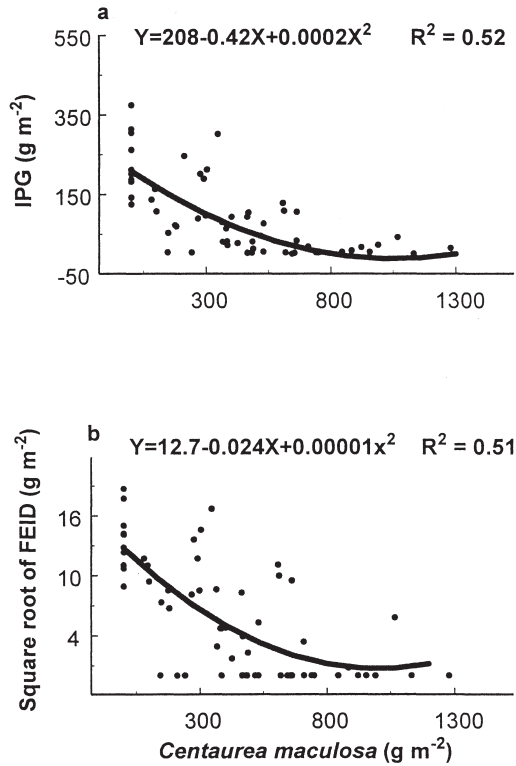
Fig. 4. Relationship between (a) indigenous perennial grass (IPG), (b) *F. idahoensis,* and *C. maculosa* and a *C. maculosa* quadratic component based on biomass. Sites were similar; regression models represent combined data.
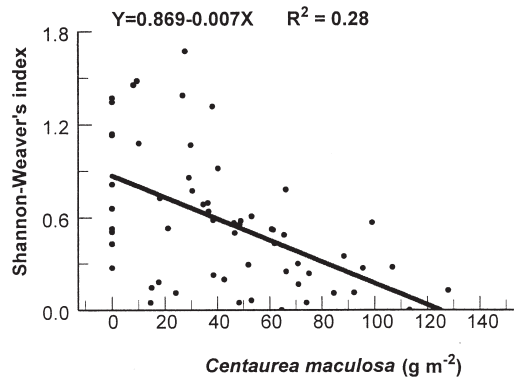

Fig. 5. Relationship between Shannon-Weaver's diversity index and *C. maculosa* based on biomass. Sites were similar; regression models represent combined data.

DISCUSSION

The invasion of semiarid rangeland by nonindigenous species is often associated with changes in plant community composition through the displacement of indigenous species (Randall 1996). This study showed species richness and diversity were inversely related to *C. maculosa* cover and biomass (Figs. 1, 5). Two plausible hypotheses explain this relationship: *C. maculosa* may displace indigenous species, or it may invade areas of low diversity and low species richness. Tyser and Key (1988) suggested that *C. maculosa* is capable of modifying plant community composition by changing species frequency. Conversely, it has been hypothesized that areas of poor species diversity result in incomplete use of limiting resources, thereby increasing invasibility by aggressive species (McNaughton 1993, Robinson et al. 1995). Tilman's (1997) observations of midwestern grasslands, that community invasibility is greater in species-poor plant communities, support this hypothesis. However, Stohlgren et al. (1999) found that, on central grasslands, patterns of exotic invasions are more closely related to degree of resources available and are independent of species richness. Individual exotic species such as *C. maculosa* may behave differently from exotic species considered as a group. Studies are needed to determine the cause of the relationship between *C. maculosa* and species richness and diversity.

We also found that occurrences of *C. maculosa* and indigenous perennial grasses are

a trend similar to indigenous perennial grasses (Fig. 4b). Indigenous forb biomass was not associated with *C. maculosa* biomass ($P \geq 0.1$).

The regression predicting species richness based on *C. maculosa* biomass was y = 4.619 – (0.015)X – (1.434)Y, R^2 = 0.38 (X = *C. maculosa* biomass, Y = average of transect within site). Differences among transects within site occurred at both sites. For each increase in *C. maculosa* biomass, Shannon-Weaver indices decreased by 0.007 (Fig. 5).

Soil Seed Bank

There were no statistical differences among species found in the seed bank at either site. *Centaurea maculosa* and *B. japonicus* were prevalent species in the seed bank at site 1 (Fig. 6a). *Bromus tectorum* was the prevalent species in the seed bank at site 2. Seeds of perennial grasses either were not present or were present at very low densities. Few indigenous forb seeds were present (Fig. 6b).
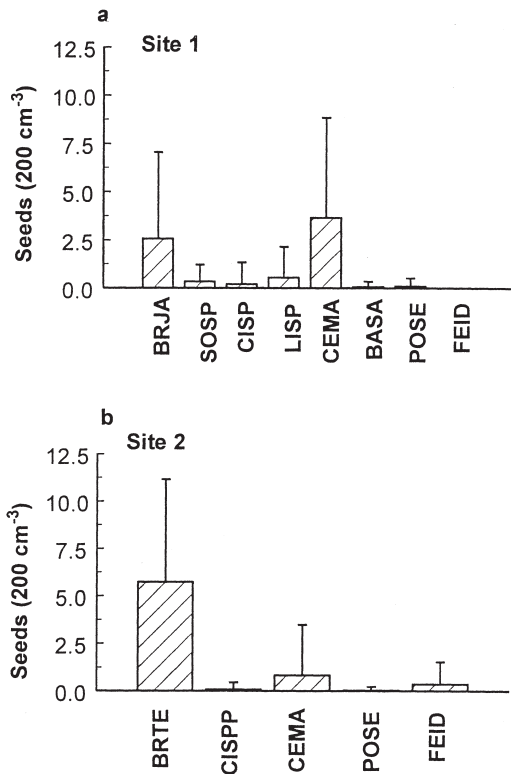
Fig. 6. Seed bank present in a 200-cm³ soil sample at (a) site 1 and (b) site 2.

inversely related (Figs. 1, 2, 4). Watson and Renney (1974) reported that declines in *P. spicatum* biomass are associated with increases in *C. maculosa* biomass. Invasive success of *C. maculosa* is attributed to rapid growth rate, prolific seed production, and high biomass (Watson and Renney 1974, Sheley et al. 1998). Seedling studies have found *C. maculosa* to be more competitive than grasses (Sheley and Jacobs 1997, Velagala et al. 1997) and indicate that *C. maculosa*'s competitive ability may allow it to dominate and displace indigenous perennial grass in some situations.

Alternatively, *C. maculosa* establishment and the apparent decline in indigenous perennial grasses may occur in areas of low grass abundance (recruitment and dispersal) where open niches exist. Tilman (1997) demonstrated that native undisturbed grasslands contain many available niches which invasive species may exploit and occupy. The lack of indigenous species found in the seed bank (Fig. 6) supports the hypothesis that *C. maculosa* may

occupy available niches left unfilled by indigenous species.

Based on temporal and spatial similarities among forbs, some cursory evidence suggests that *C. maculosa* directly competes with indigenous forbs (Jacobs and Sheley 1999). In our study no relationship was detected between *C. maculosa* density, cover, or biomass, and forb density, cover, or biomass. In a study to assess herbicide impacts on nontarget species, Rice and Toney (1996) reported that forb (e.g., *A. holboellii, B. sagittata, H. villosa*) cover in control plots remained constant over time for 3 of 4 important species in areas of early to intermediate stages of *C. maculosa* invasion. Some indigenous rangeland forbs may not occupy the same niche as *C. maculosa.* This is surprising, because Sheley and Larson (1996) indicated that *Centaurea diffusa* Lam. can occupy all available niches by developing a hierarchy of age classes. These results may not apply to spring ephemeral forbs, which this study did not consider.

Models predicting *F. idahoensis* density, cover, and biomass based on *C. maculosa* density, cover (Fig. 2), and biomass (Fig. 4), respectively, demonstrated a sharp decline in *F. idahoensis* followed by its low-level persistence at higher levels of *C. maculosa* (>350 plants m^{-2}, $>55\%$ cover, and >550 g m^{-2}). One objective of land managers in treating *C. maculosa* infestations with herbicides includes returning rangeland to pre-invasion levels of desirable grass species. It is recommended that land managers consider the understory of residual grass species that is available to respond to management before weed management decisions are made (Sheley and Jacobs 1997). This knowledge could potentially help land managers predict levels of perennial grasses necessary to return a *C. maculosa*–infested area to a desired perennial grass–dominated community.

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