

## Spotted Knapweed (*Centaurea biebersteinii* DC) Response to Forest Wildfires on the Bitterroot National Forest, Montana

### Abstract

The 2000 Bitterroot wildfires in Montana burned 124,250 ha of forest and rangelands on the Bitterroot National Forest. Because spotted knapweed (*Centaurea biebersteinii* DC) is common on the Bitterroot National Forest, there is a high potential of expanded knapweed populations following the wildfires. A stratified random sample was used to study forest vegetation development following the wildfires. A total of 283 plots in 71 stands were measured three times during the 5-year period after burning. Knapweed occurred on 19.4% of plots at 1 or 2 years postfire, 26.1% at 3 years, and 37.1% at 5 years. Occurrence at 5 years was higher on Douglas-fir [*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco] habitat types (56.0%) than on subalpine fir [*Abies lasiocarpa* (Hook.) Nutt.] habitat types (9.6%). Initially after the fire, occurrence and cover of knapweed were inversely correlated with forest floor burn severity; however, the rate of increase over time was higher at higher burn severities. Knapweed cover declined over time on plots with low burn severity and increased over time on plots with high burn severity. Knapweed was tallest on plots where it first occurred at year 3 and shortest where it first occurred at year 5. Collectively, these results suggest that vegetation recovery is important for reducing knapweed populations, especially on Douglas-fir habitat types.

### Introduction

Wildfires were a major agent of change in northern Rocky Mountain forests prior to organized fire protection (Arno 1980). In recent years, crown fires that killed much of the overstory have become more common in some dry western U.S. forests, while low severity ground fires that burned the understory but killed few overstory trees have become less common (Steele et al. 1986, Covington and Moore 1994). Fire exclusion and suppression may have promoted increased fuel loads and fuel connectivity (Auclair and Bedford 1994). Hessburg et al. (2000) document vegetation changes during the period 1932 to 1993 for interior northwest U.S. forests. They discuss expansion of forests, increasing connectivity of forests, shifts from early to late seral conifers, and increased risk of stand replacing wildfires.

Large uncontrolled wildfires provide opportunities to conduct research that we could not afford, nor would we be allowed to conduct. The 2000 Bitterroot wildfires burned 144,100 ha of forest and rangelands on public and private lands in Montana (Bitterroot NF 2000). A July 31 dry lightning storm started 78 fires that grew together into several major complexes. On the Bitterroot National Forest (NF), 124,250 ha were burned with

a wide range of burn severities across all habitat and moisture regimes (Bitterroot NF 2000).

Understanding vegetation dynamics following wildfire is important for several reasons. Vegetation recovery is linked to soil erosion, watershed quality and quantity, and wildlife values (Robichaud et al. 2000, Wondzell and King 2003). A major concern for western U.S. forests is invasive plant species following wildfires that alter the ecology of forests and result in economic losses (Perrings et al. 2002, Evans 2003, Strauss et al. 2006). The Chief of the Forest Service has identified invasive plants as one of four major threats to Forest Service land (Bosworth 2004).

The most common invasive species on the Bitterroot NF is spotted knapweed (*Centaurea biebersteinii* DC [= *C. maculosa* Lam.]) -- a short-lived perennial composite that is native in central Europe and Asia Minor (Sheley et al. 1998). It occurs in every county in Montana (Sheley et al. 1998) and potentially threatens 40% (15 million ha) of the state (Chicoine et al. 1985). Knapweed primarily invades semiarid pastures and rangelands (Jacobs and Sheley 1998), but it can also invade low elevation forests (Forcella and Harvey 1983, Roche and Roche 1988). Most forested areas on the Bitterroot NF that are located on south facing slopes, with less than 40% tree cover, and below 2,000 m elevation have populations of knapweed (Bitterroot NF 2000).

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Soil disturbance is associated with successful establishment of spotted knapweed (Watson and Renney 1974, Forcella and Harvey 1983). Expansion of knapweed colonies occurs through germination of seed along the periphery of stands, which may be aided by allelopathic compounds (Bais et al. 2003). Knapweed does not compete well in moist areas, such as near wet microsites or in irrigated fields (Harris and Cranston 1979, Powell et al. 1997). Burning can reduce population growth (Abella and MacDonald 2000, Emery and Gross 2005), but it does not control knapweed (Sheley et al. 1998). Burning can also facilitate colonization of knapweed by decreasing competition and providing microsites for seedling establishment (Sheley et al. 1998, Emery and Gross 2005). Measures to reduce knapweed populations include hand weeding, plowing, selective animal grazing, herbicides, biological control, and revegetation (Sheley et al. 1998). Researchers and managers are recognizing the need for an integrated approach to knapweed management to promote healthy plant communities that compete well against knapweed (Tyser and Key 1988, Sheley et al. 1998, LeJeune and Seastedt 2001).

The objective of this paper is to quantify the relationships between spotted knapweed and site conditions for the first 5 years following wildfires on the Bitterroot NF. This study is part of a larger study on vegetation recovery following wildfires in the northern Rocky Mountains. We have 5 years of data from the 2000 Bitterroot fires, which are the oldest wildfires in our study.

## Methods

### Study Design

A stratified random sample was used to select stands within the 2000 burn perimeter on the Bitterroot NF. Stratification insured a range of conditions was sampled, using combinations of:

- Two prefire cover types (Douglas-fir/ponderosa pine [*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco/*Pinus ponderosa* Dougl. ex Laws. var. *ponderosa*]; subalpine fir/lodgepole pine [*Abies lasiocarpa* (Hook.) Nutt./*Pinus contorta* Dougl. ex Loud.]),
- Two burning index classes ( $<75$ ;  $\geq 75$ ), an index of predicted fire spread and energy release (Bradshaw et al. 1983),

- Two slope steepness classes ( $\leq 35\%$ ;  $> 35\%$ ),
- Two prefire canopy heights ( $\leq 12$  m;  $> 12$  m tall), and
- Two prefire stand densities ( $\leq 35\%$ ;  $> 35\%$  conifer canopy cover).

Over 6,000 stands were classified into the stratification matrix, but all combinations were not possible. Within each combination of stratification variables, three low density stands were randomly selected for sampling.

The center for the first plot was determined by drawing transect lines on aerial photographs that intersected at the approximate center of the stand, and assigning a GPS point. Field crews located this GPS point and installed a 4-point cluster of plots. Crews then installed a second 4-point cluster in an adjacent stand within the burn perimeter that had a higher prefire density. Only in a few instances were we unable to find an acceptable adjacent stand.

Our sampling design is similar to that used by Forest Inventory and Analysis (FIA) (Bechtold and Scott 2005). The first point is in the center, the second at an azimuth of  $0^\circ$ , the third at  $120^\circ$ , and the fourth at  $240^\circ$ . Points 2, 3, and 4 are 36.5 m from point 1. Each point has three plots associated with it. First is a  $13.5 \text{ m}^2$  circular plot to record vegetation, slope, aspect, and burn severity for the forest floor, low shrubs, and tall shrubs. Second is a  $168 \text{ m}^2$  circular plot to record habitat type (Pfister et al. 1977) and burn severity for overstory trees. Third is a variable radius plot for sampling overstory trees.

Plots were initially measured in 2001 or 2002 (measure 1), and then remeasured in 2003 (measure 2) and 2005 (measure 3). Field sampling was done in late June through August, beginning at low elevations where the growing season started earlier and progressing upward as vegetation developed at higher elevations. Vegetation dried earlier than usual in 2001, so we were unable to record vegetation for 25 stands. For these stands, burn severity was recorded and overstory trees were selected and measured in 2001, and vegetation was recorded in 2002.

Stand elevation was recorded at plot 1, which was the only variable recorded at the stand level. All other variables were recorded at the plot level to make plots as independent as possible. Vegetation abundance was estimated using Daubenmire's

(1959) ocular estimate of canopy coverage, except we used 13.5 m<sup>2</sup> circular plots instead of rectangular plots and we recorded percentages rather than cover classes. Percent cover of shrubs, forbs, grasses, and ferns was recorded as lifeforms. Percent cover of invasive plants was recorded for each species, and heights (nearest 15 cm) were recorded in 2005. In order to determine heights for each species, field crews mentally averaged plants of different sizes, shapes, and coverages without disturbing the vegetation; therefore, 15 cm increments are considered reasonably accurate.

Burn severity classes were used to characterize the effects of fire on vegetation and soil. Classes were recorded for each of four strata (forest floor, short shrubs, tall shrubs, and overstory trees) using the following categories: 0=unburned, 1=light (blackened duff, scorched foliage, overstory trees predominately green and/or brown needles), 2=moderate (duff consumed, shrubs mostly consumed but stubs remaining, overstory trees predominately brown and/or burned needles), and 3=severe (mineral soil colored orange, shrubs totally consumed leaving holes in the soil, and overstory trees predominately black). Each burn severity class was recorded by percent of the plot that it occupied; e.g., 30% severe burn and 70% moderate burn to the forest floor.

Overstory trees were sampled to quantify prefire overstory density and postfire overstory competition. Basal area factors of 2.3, 4.6, or 9.2 m<sup>2</sup> ha<sup>-1</sup> were used to sample five to seven trees or snags per plot.

## Data Analyses

Our modeling technique uses methods applicable to two-state systems described by Hamilton and Brickell (1983). The first step is to predict the probability of spotted knapweed occurrence—it either occurs on the 13.5 m<sup>2</sup> plot or it does not. All plots are used to estimate the probability of occurrence. The second step is to predict attributes for plots where the species occurs; e.g., percent cover and height. Equations will be used in the Fire and Fuels Extension to the Forest Vegetation Simulator (Reinhardt and Crookston 2003) to predict vegetation recovery following wildfires.

Preliminary analyses showed that habitat types could be combined into two groups: (1) the Douglas-fir and ponderosa pine habitat type series (hereafter called Douglas-fir series and

labeled PSME series in tables and figures), and (2) the subalpine fir and Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) series (hereafter called subalpine fir series and labeled ABLA series in tables and figures). The Douglas-fir series is relatively warm and dry, and supports conifers such as ponderosa pine, Douglas-fir, lodgepole pine, and western larch (*Larix occidentalis* Nutt.). The subalpine fir series is cool and moist, and supports subalpine fir, Engelmann spruce, and lodgepole pine.

Burn severity indices were calculated for each plot. The burn severity codes (0, 1, 2, and 3) were weighted by the proportion of the 13.5 m<sup>2</sup> plot they occupied. Preliminary analyses showed that forest floor burn severity (ffsev) was the best predictor of spotted knapweed compared to burn severity for low shrubs, tall shrubs, or overstory trees.

The interaction of aspect and slope was modeled as suggested by Stage (1976). Stage's technique allows the calculation of the optimum aspect from the regression coefficients.

Data were analyzed using methods for mixed models in SAS 9.1 (Littell et al. 1996). The probability of spotted knapweed occurrence was estimated with PROC GLIMMIX using a dichotomously distributed dependent variable (1 if knapweed occurs and 0 otherwise). The predicted probability is continuous and bounded in the interval [0,1]. PROC MIXED was used to predict knapweed cover and height. Analyses specified repeated measures to account for the correlation of measuring the same plots at three successive time periods. The SUBJECT statement was used to account for the correlation among plots within stands; SAS then accounts for the correlation to construct the appropriate test statistics.

Statistical significance of independent variables was assessed at  $P = 0.05$ . Transformations of variables were explored to achieve homogeneity of error variance, normality of error and block effects, and to obtain additivity of effects.

## Results

Seventy-one stands were measured, with four plots per stand, for a total of 284 plots. We inadvertently missed measuring one plot in 2003, so all data for this plot were withheld from the analyses. Stand locations are shown in Figure 1.

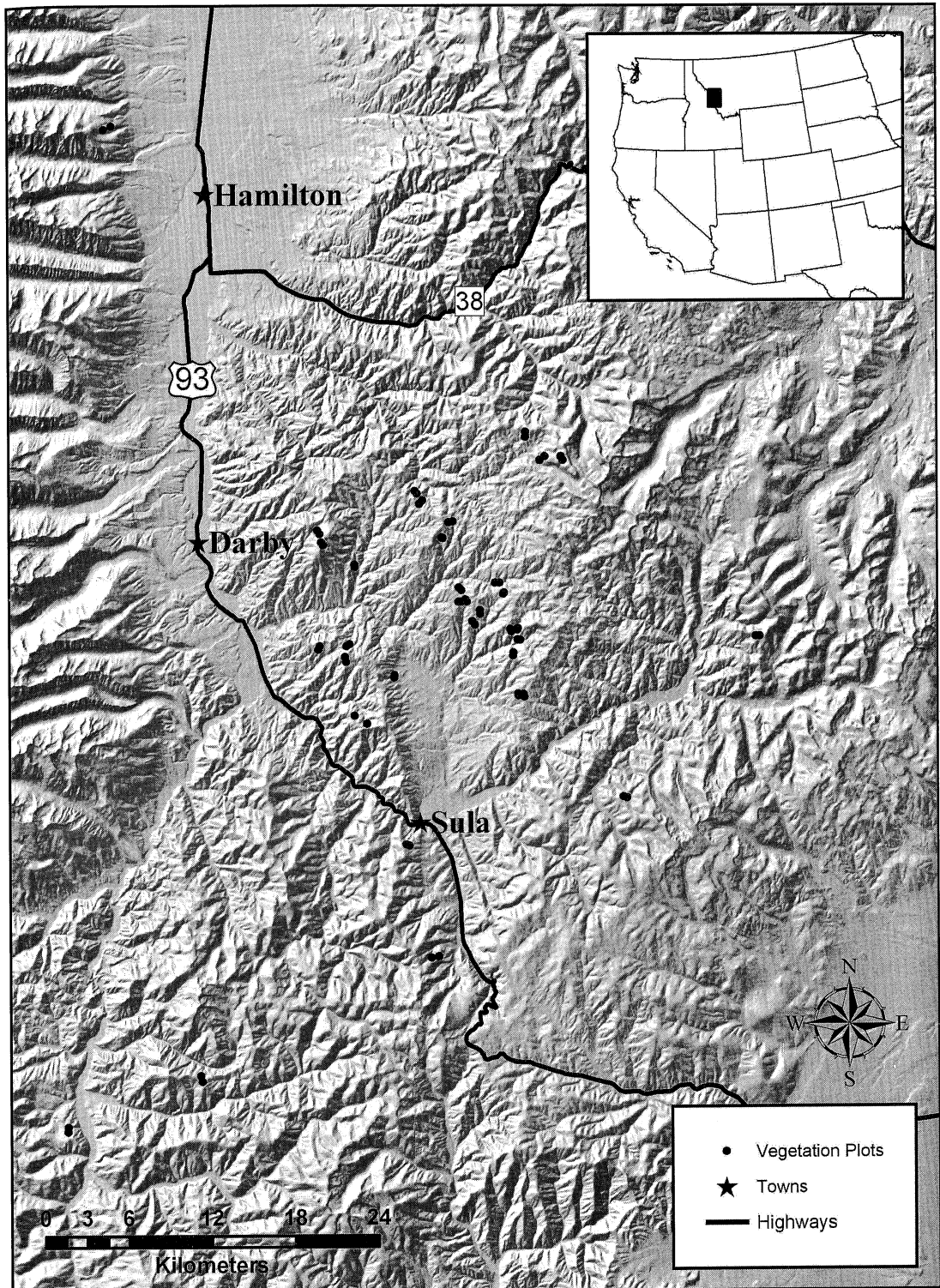


Figure 1. Locations of 71 sample stands.

## Occurrence of Spotted Knapweed

Spotted knapweed occurred on 55 of 283 plots (19.4%) during the first measure, 74 plots (26.1%) in year 3, and 105 plots (37.1%) in year 5. The occurrence of knapweed on the Douglas-fir habitat type series (56.0% at year 5) was much higher than on the subalpine fir series (9.6% at year 5).

Table 1 shows spotted knapweed occurrence by habitat type series and three classes of forest floor burn severity. Three forest floor burn severity classes were chosen that had approximately equal numbers of observations (0 to 0.5,  $\geq 0.5$  to 1.5, and  $\geq 1.5$ ). Three trends are clear in Table 1. First, occurrence of knapweed is much higher on the Douglas-fir vs. the subalpine fir series. Second, increasing forest floor burn severities had decreased occurrence at the first measure. Third, the rate of increase in occurrence over time is more rapid for higher forest floor burn severities than for lower burn severities.

TABLE 1. Occurrence of spotted knapweed by burn severity to the forest floor (ffsev), measure, and habitat type series (PSME is the Douglas-fir habitat type series and ABLA is the subalpine fir series).

ffsev	1	Measure 2	3	Number of plots
PSME series				
0.0 to 0.5	0.571	0.510	0.633	49
$\geq 0.5$ to 1.5	0.277	0.462	0.569	65
$\geq 1.5$	0.111	0.222	0.481	54
ABLA series				
0.0 to 0.5	0.056	0.056	0.056	18
$\geq 0.5$ to 1.5	0.022	0.089	0.156	45
$\geq 1.5$	0.019	0.038	0.058	52
All data				
0.0 to 0.5	0.433	0.388	0.478	67
$\geq 0.5$ to 1.5	0.173	0.309	0.400	110
$\geq 1.5$	0.066	0.132	0.274	106

Probability of occurrence for spotted knapweed is shown in Table 2, and Figure 2 shows the results of exercising the equation. Results of regression analyses confirm the trends apparent in Table 1. Increasing burn severity to the forest floor decreases the initial probability of knapweed, but knapweed increases more rapidly over time at higher burn severities. The subalpine fir habitat type series has a significantly lower probability of knapweed than the Douglas-fir series, and

TABLE 2. Regression coefficients for estimating the probability of occurrence for spotted knapweed on 13.5 m<sup>2</sup> plots for the first 5 years following wildfire. The form of the equation is  $PROB = (1 + e^{-(\sum \beta_i X_i)})^{-1}$ , where "e" is the base of natural logarithms.

Variable (X)	Coefficient (B)	Units
constant	8.9097	
PSME series	0.0	categorical
ABLA series	-2.1004	categorical
elevation	-0.4518	m/100
time	0.0969	years since wildfire
ffsev	-1.6092	weighted average
ffsev*time	0.2250	
cos(aspect)*slope	-0.2490	slope %/100
sin(aspect)*slope	-1.0846	
basal area	-0.0472	m <sup>2</sup> ha <sup>-1</sup>
chi-square/ degrees of freedom	1.08	

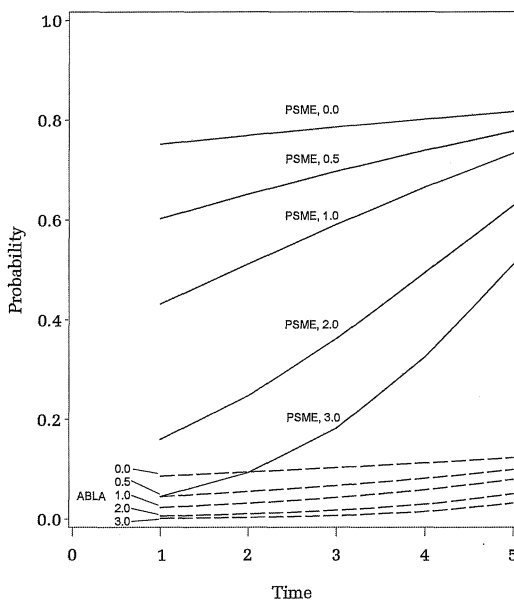


Figure 2. Probability of occurrence for spotted knapweed using the regression equation shown in Table 2. The solid lines are for the Douglas-fir habitat type series, 1700 m elevation, and forest floor burn severities of 0.0, 0.5, 1.0, 2.0, and 3.0 (from top to bottom). The dashed lines are for the subalpine fir series, 2000 m elevation, and the same sequence of burn severities.

increasing elevation decreases the probability of knapweed. The probability of knapweed is highest at 254° azimuth.

TABLE 3. Average percent cover of spotted knapweed on plots where it occurred, by time since the wildfire and year that knapweed first occurred on plots, and average knapweed height at year 5. Numbers in parentheses are number of plots, and numbers in brackets are average forest floor burn severity.

First occurrence	Cover (%)			Heights (m)
	Year 1 or 2	Year 3	Year 5	Year 5
2001/2002	10.6 (55) [1.68]	11.9 (50) [1.72]	13.4 (50) [1.72]	0.45 (50) [1.72]
2003		1.5 (24) [2.28]	7.7 (21) [2.31]	0.54 (21) [2.31]
2005			1.3 (34) [2.34]	0.39 (34) [2.34]
All data	10.6 (55) [1.68]	8.5 (74) [1.84]	8.3 (105) [1.97]	0.45 (105) [1.97]

### Percent Cover of Spotted Knapweed

Percent cover estimates the size of spotted knapweed populations. At the first measure, knapweed cover was 10.6% on 55 plots (Table 3). In year 3, only 50 of these 55 plots still had knapweed, and average cover increased to 11.9%. In year 3, average knapweed cover was 1.5% on an additional 24 plots that did not have knapweed at the first measure. In year 5, average knapweed cover increased from 11.9% to 13.4% on plots that had knapweed at the first measure. Cover increased from 1.5% to 7.7% on plots that had knapweed for the first time at year 3. Also by year 5, knapweed cover was 1.3% on an additional 34 plots. Average burn severity increased with increasing delay in knapweed occurrence—1.68 for plots that had knapweed at the first measure, 2.28 for plots that knapweed first occurred at year 3, and 2.34 for plots that knapweed first occurred at year 5.

Note that the presentation of data by knapweed's first occurrence avoids misleading and counterintuitive results. Simple averages of percent cover at the bottom of Table 3 would indicate that knapweed decreases over time (10.6% at year 1 or 2, 8.5% at year 3, and 8.3% at year 5).

The change in percent cover of spotted knapweed over time differs by burn severity. We defined three classes for the forest floor burn severity index (0 to 0.5,  $\geq 0.5$  to 1.5, and  $\geq 1.5$ ) and calculated

TABLE 4. Regression coefficients for estimating percent cover of spotted knapweed on 13.5 m<sup>2</sup> plots for the first 5 years following wildfire. The form of the equation is  $\text{COVER} = e^{(\sum \beta_i X_i)}$ , where "e" is the base of natural logarithms.

Variable (X)	Coefficient ( $\beta$ )	Units
constant	5.1322	
elevation	-0.2321	m/100
ffsev	-0.9923	weighted average
ffsev*time for PSME series	0.1721	time = years since wildfire
ffsev*time for ABLA series	0.1090	
ln(basal area)	-0.3391	m <sup>2</sup> ha <sup>-1</sup>
covforb	-0.0184	% cover
occur first measure	1.7366	categorical
occur second measure	1.0003	
occur third measure	0.0	
cos(aspect)*slope	-0.6136	slope %/100
sin(aspect)*slope	-0.9763	

the changes in percent cover between the first and third measures. The lowest burn severity class (0 to 0.5) had an average change in cover of -3.4%, the moderate burn severity class ( $\geq 0.5$  to 1.5) had an average change of +4.5%, and the highest burn severity class ( $\geq 1.5$ ) had an average change of +6.4%.

Regression analysis of percent cover showed that increasing percent cover of competing forbs was associated with decreasing cover of spotted knapweed (Table 4). Increasing overstory basal area was also associated with decreased knapweed cover. Knapweed cover decreased with increasing elevation, and it decreased with increasing time between the wildfire and knapweed occurrence. Higher forest floor burn severity resulted in lower initial cover of knapweed, but cover increased more rapidly over time for higher burn severities. Predicted knapweed cover is highest at 237° azimuth.

### Heights of Spotted Knapweed

Average height of spotted knapweed at 5 years was 0.45 m on plots where knapweed occurred at the first measure (Table 3). Knapweed was tallest (0.54 m) on plots where it first occurred at year 3. Knapweed was significantly shorter (0.39 m) where it first occurred at year 5.

Regression analysis showed that increasing elevation and increasing overstory basal area were



associated with decreasing spotted knapweed heights (Table 5). Also, the order of predicted heights, based on when knapweed first occurred, agrees with the order in Table 3. Average heights were not significantly different between plants that occurred during the first and second measure ( $P=0.064$ ).

TABLE 5. Regression coefficients for estimating heights of spotted knapweed 5 years after wildfire. The form of the equation is  $HT = \sum \beta_i X_i$ .

Variable (X)	Coefficient ( $\beta$ )	Units
constant	1.1674	
elevation	-0.0420	m/100
ln(basal area)	-0.0321	m <sup>2</sup> ha <sup>-1</sup>
occur first measure	0.0815	categorical
occur second measure	0.1496	
occur third measure	0.0	

## Discussion

Results from this study quantify the response of spotted knapweed to wildfire in forest environments, and they verify observations from previous research. Subalpine fir habitat types have a much lower probability of knapweed than Douglas-fir habitat types. Westerly aspects have the highest probability of knapweed, and increasing elevation decreases the probability of knapweed. Higher burn severity to the forest floor is correlated with lower probabilities of knapweed occurring at the first measure. Over time, plots with higher burn severities have higher rates of invasion than plots that have lower burn severities. It is likely that high surface temperatures kill knapweed plants and destroy seed stored in the soil (Abella and MacDonald 2000, Emery and Gross 2005), but it is also likely that wildfires facilitate knapweed invasion by decreasing competition and providing microsites for seedling establishment (Sheley et al. 1998, Emery and Gross 2005). Five years after the fire, the occurrence of knapweed on higher burn severities is catching up with lower burn severities. Future remeasurements will provide data to determine if more knapweed will eventually occur on higher burn severities than lower burn severities.

Percent cover and heights of spotted knapweed decrease with increasing elevation. Cover and heights decrease when there is a delay between

the wildfire and seedling establishment. Knapweed cover decreases with increasing overstory basal area and forb cover. Initial cover decreases with increasing forest floor burn severity, but increases more rapidly over time for higher burn severities. There is an interesting trend of decreasing knapweed cover over time at lower burn severities and increasing cover at higher burn severities.

The results of this study agree with Forcella and Harvey (1983) who surveyed spotted knapweed populations along an elevational transect (warm-dry steppe through cool-moist subalpine fir forests) about 85 km from our study sites. They concluded that knapweed could invade grasslands and ponderosa pine habitat types without site disturbance. Douglas-fir habitat types were invaded by knapweed if there was site disturbance, but relatively undisturbed native vegetation was not invaded. Subalpine fir habitat types were almost never invaded whether or not there was site disturbance.

Our findings correlate well with mechanisms that are thought to control the distribution of spotted knapweed—soil disturbance, amount of sunlight reaching the herbaceous layer, and climate. First, increasing soil disturbance is correlated with increasing knapweed colonization (Watson and Renney 1974, Forcella and Harvey 1983, Sheley et al. 1998). Second, knapweed occurs in sun-saturated environments where sunlight reaches the herbaceous layer, while knapweed does poorly when shaded (Watson and Renney 1974, Forcella and Harvey 1983). Third, knapweed is most common in semiarid rangelands and in habitats dominated by ponderosa pine and Douglas-fir (Watson and Renney 1974, Chicoine et al. 1985). Forcella and Harvey (1983) note a marked increase in knapweed in ponderosa pine and grassland habitats that have three months with one or no frosts compared to mid-montane and subalpine fir habitats that have no months without frosts.

The results of our study, coupled with those of Forcella and Harvey (1983), can be used to develop an integrated strategy to combat spotted knapweed following wildfires that considers habitat types and emphasizes the need to revegetate disturbed sites. Knapweed occurrence is quite low on subalpine fir habitat types where it does not readily invade, with or without disturbance. This agreement between two studies in the same vicinity, about 20 years apart, suggests that knapweed is not expanding

to subalpine fir habitats. Therefore, subalpine fir habitat types are not a priority concern for knapweed invasion following wildfires.

On Douglas-fir habitat types, disturbance is a prerequisite for spotted knapweed invasion; therefore, Douglas-fir habitat types are a priority for knapweed management following wildfire. Reestablishment of native vegetation is important for decreasing knapweed populations on Douglas-fir habitat types. This recommendation is supported by Forcella and Harvey (1983), who found that knapweed does not readily invade undisturbed vegetation on Douglas-fir habitat types, and our finding that knapweed cover is decreasing over time where forest floor burn severity was low. Quickly reestablishing native vegetation would also be beneficial for reducing erosion and keeping nutrients on site following wildfires.

Our recommendations for ponderosa pine habitat types are based on the research of Forcella and Harvey (1983) because we have only seven plots in the ponderosa pine series. Ponderosa pine habitat types are readily invaded by knapweed, and disturbance is not a prerequisite to invasion or colony expansion. It is very likely that ponderosa pine habitat types had established populations of knapweed before the wildfire (Bitterroot NF 2000). Fire would temporarily decrease knapweed populations by killing plants and destroying seed in the soil, but fire is also a disturbance agent that

facilitates knapweed colonization and expansion. Reestablishment of native vegetation could help manage expansion of knapweed populations, but knapweed will continue to occupy ponderosa pine habitat types with or without disturbance.

The idea of prioritizing efforts to combat spotted knapweed after wildfires based on habitat types and burn severity has merit. Rapid revegetation with native plants would be most beneficial on Douglas-fir habitat types, especially where burn severity was higher. Revegetation would likely be beneficial on ponderosa pine habitat types, while subalpine fir habitat types are not at great risk of knapweed invasion. A useful refinement would be to have more information by individual habitat types. For instance, it seems logical that knapweed would invade dry Douglas-fir habitat types more readily than moist Douglas-fir habitat types. Management of other invasive plant species may also benefit by understanding their ability to invade different habitat types.

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