THE RESPONSE OF A SPOTTED KNAPWEED DOMINATED COMMUNITY TO SELECTIVE DEFOLIATION AT DIFFERENT PHENOLOGIES

A Thesis

Presented in Partial Fulfillment of the Requirements for the

Degree of Master of Science

with a

Major in Rangeland Ecology and Management

in the

College of Graduate Studies

University of Idaho

by

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November 2009

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Abstract. Spotted knapweed (*Centaurea stoebe* L.) is a perennial invasive plant that has infested millions of hectares in North America. Grazing animals have often been used to manage vegetation communities for habitat improvement, community alteration, and other goals, including weed control. Research on spotted knapweed management has shown that defoliation through grazing, clipping, and mowing can control spotted knapweed. However, few have studied the mechanisms that allow grazing to successfully control spotted knapweed in a community context. This study investigates the response of spotted knapweed basal cover, density, mortality, and flower production and basal cover and density of the associated vegetation to defoliation at various phenological stages and repeated defoliation. Defoliation treatments consisted of defoliating the spotted knapweed only, the associated vegetation only, all vegetation or an unclipped control at the rosette, bolting, or flowering phenology, or a repeated rosette flowering treatment. Our results show that greater spotted knapweed mortality and lower flower production when it was clipped than when it was not ($p<0.01$), with greater mortality occurring in the rosette stage or the repeated defoliation treatment than in the bolting or flowering stages ($p<0.01$), with no effects to the associated perennial grasses. Our study also indicates that, though there was minimal effects to perennial grasses, longer periods of defoliating everything but spotted knapweed can increase flower production. The density of large robust forbs, such as arrowleaf balsamroot (*Balsamorhiza sagittata* [Pursh] Nutt.) and tapertip hawksbeard (*Crepis acuminata* Nutt.) was shown to be sensitive to defoliation ($p<0.01$), particularly during the rosette and bolting phenology and to repeated defoliation ($p=0.02$). Annual grasses showed an increase in basal cover and density when only spotted knapweed was clipped, compared to other treatments ($p=0.01$; $p=0.02$, respectively). Annual forbs were unaffected by defoliation treatment at any phenological stage. Our results indicate that spotted knapweed can be controlled through defoliation either alone, or in conjunction with the associated vegetation community, with minimal effects to the associated grass community. However the plant community must be considered, allowing for the reaction of each component to the selectivity of the defoliating agent.

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Chapter I: Overview of Biology and Control of Spotted Knapweed with Focus on Plant Response to Defoliation

Invasive weeds are a serious and expanding rangeland problem in North America (Mullin et al. 2000). These exotic plants compete with native vegetation for resources and can alter plant community composition, structure, and function (Belcher and Wilson 1989; DiTomaso 2000). Invasive weeds have been shown to increase soil erosion rates (Lacey et al. 1989), displace native plant species (Olson 1999), reduce herbivore use (Hein and Miller 1992), and reduce site productivity and biodiversity (Lacey et al. 1989; Sheley and Jacobs 1996; Trammell and Butler 1995).

Spotted Knapweed Natural History and Growth Characteristics. Spotted knapweed (*Centaurea stoebe* L.[1]) is an invasive weed, first introduced to North America in the late 1800s from Eurasia through discarded soil that was used as ship ballast (Muller et al. 1988; Sheley et al. 1998). Recent estimates of spotted knapweed range include seven Canadian Provinces and forty six states, including every county in Oregon, Washington, Idaho, and Montana (USDA, NRCS 2009). Spotted knapweed produces a deep taproot that supports a basal rosette of leaves and several stems that branch at the upper part of the stem into flowering stalks that bear purple to pink composite flowers heads characteristic of plants from the Asteraceae family (Sheley et al. 1998).

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[1] Plant names follow those suggested in the U.S. Department of Agriculture, Natural Resource Conservation Service PLANTS database at: http://www.plants.usda.gov/.

Spotted knapweed is a short-lived perennial that lives for up to nine years (Boggs and Story 1987). Plants are capable of producing seeds in its first year and each subsequent year of growth (Shirman 1981; Boggs and Story 1987). Spotted knapweed is a prolific seed producer capable of producing 5,000 to 40,000 seeds per square meter (Boggs and Story 1987). Seeds can persist in the soil up to seven years (Sheley et al. 1998).

Spotted knapweed germinates in the fall and spring when soil moisture and ambient temperatures are favorable (Watson and Renney 1974). Seedlings form rosettes in the early spring with maximum root growth occurring at this time (Watson and Renney 1974). Root crowns from mature plants also produce rosettes in spring with plants bolting in early May, and flowering from June through September (Sheley et al. 1998). Mature seeds begin to form in mid-August and are primarily dispersed by wind (Sheley et al. 1998).

Ecological Impacts of Spotted Knapweed. As spotted knapweed invades and comes to dominate a site, it can cause a shift in plant community composition, resulting in lower biodiversity (Tyser and Key 1988). Vegetative cover at the soil surface can also be reduced yielding increased soil erosion and reduced water quality in infested areas. In one study, runoff was 56% greater and sediment yield was 192% higher in spotted knapweed dominated sites compared to control sites (Lacey et al. 1989).

Spotted knapweed can displace native vegetation and reduce forage for herbivores. In a study in southern British Columbia, spotted knapweed infestation reduced bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] A. Löve) and rough fescue (*Festuca campestris* Rybd.) production by 87% (Watson and Renney 1974). This reduced the stocking rate from 0.61 ha per Animal Unit Month (AUM) to 4.86 ha per AUM. In a western

Montana study, Rice et al. (1997) found a reduction in elk forage of up to 47%. Other studies have shown that spotted knapweed is readily consumed by deer and elk and may be a valuable forage resource. Mule deer along the Selway River in Idaho were observed eating large quantities of spotted knapweed rosette leaves, and elk would eat them frequently, but in lesser quantities (Wright and Kelsey 1997). In this study, seedheads were also consumed frequently when snow cover reduced the availability of other forage. However, lack of available native forage had probably limited their choices.

Cattle, sheep and goats are known to consume spotted knapweed (Sheley et al. 1998) and spotted knapweed can also be valuable forage for wildlife and livestock (Wright and Kelsey 1997; Olson and Wallander 2001; Hale 2002). Plants contain adequate nutritive value to meet livestock needs throughout the growing season (Kelsey and Mihalovich 1987). Crude protein levels of spotted knapweed decrease throughout the growing season (from 20 to 11%) with fiber content increasing (from 25 to 40%) as the plant matures (Ganguli et al. In Press).

Control Methods. Methods to control spotted knapweed include: biological, burning, cultivation, grazing, hand pulling, herbicides, mowing, and revegetation (Sheley et al. 1998). While these control methods have shown success in controlling small infestations of spotted knapweed, widespread control of spotted knapweed has not been successful (Olson et al. 1997).

Biological Control. There are thirteen biological control insects that have been used to manage spotted knapweed (Wilson and Randall 2005). These insects generally impact either the seed head or roots of the target plants (Sheley et al. 1998; Wilson and Randall 2005; Story et al. 2008). Two seed head gall-producing flies (*Urophora affinis* and *U. quadrifasciat*) are well established in the United States, and the larvae of these flies have been shown to reduce seed production by up to 50% (Story et al. 1989). Another species, *Cyphocleonus achates*, has also been shown to be successful in controlling spotted knapweed (Knochel and Seastedt 2009). The success of many of the other insects in controlling spotted knapweed, however, has not been quantified. One study even contends that the root boring moth *Agapeta zoegana* may increase the competitive ability of spotted knapweed by stimulating secondary growth or production of allelopathic compounds (Callaway et al. 1999).

Biological weed control agents have been proven to be useful, but multiple agents have been found to be necessary for effective control (Wilson and Randall 2005), and maintenance of biological control agent populations has proven to be problematic. For example, predation on spotted knapweed gall fly populations has been shown to effectively reduce population of this fly (Pearson et al. 2000). Another problem with biological control agents is that dense knapweed infestations are generally required to maintain adequate populations (Wilson and Randall 2005).

Herbicides. Several experiments examining the effects of different herbicides on invasive weeds demonstrate that a certain level of weed control is obtained when treated with herbicides such as picloram (Lym and Messersmith 1986; Whitson et al. 1986), 2,4-D (Lym and Messersmith 1986; Sheley et al. 2000; Whitson et al. 1986), clopyralid, dicamba (Sheley et al. 2000; Whitson et al. 1986). The most widely used herbicides for spotted knapweed control are picloram and clopyralid + 2,4-D (Prather 2007).

Effectiveness of most herbicides depends on timing of treatment, residual effect of the herbicide, and soil conditions (Sheley et al. 1998). Clopyralid and clopyralid + 2,4-D are most effective when used during the bud or bolting stages of knapweed (Lacey et al. 1995). Dicamba has no residual effect, therefore must be applied annually to result in any long-term control (Sheley et al. 1998). Picloram appears to be one of the most effective herbicide for knapweed control, due to its longer residual effect and its ability to control knapweed at any actively growing stage.

Defoliation by Mowing and Grazing. Mowing has been shown to decrease spotted knapweed cover and density without affecting the associated grass community (Rinella et al. 2001). Mowing can also reduce seed production and germination (Watson and Renney 1974). In greenhouse studies, however, spotted knapweed was shown to be less sensitive to defoliation than bluebunch wheatgrass (Kennett et al. 1992).

Grazing animals have often been used to manage vegetation communities for habitat improvement, community alteration, and other goals, including weed control (Frost and Launchbaugh 2003). Olson and Wallander (1998) were successful in reducing leafy spurge (*Euphorbia esula* L.) density and the viable seed in the seed bank by grazing with sheep, and had minimal effect on cool-season native grasses. Similarly, Olson et al. (1997) successfully reduced the reproductive output of leafy spurge with sheep grazing. Grazing by sheep (Hovde 2006) and goats (Goehring 2009) have been shown to be effective in controlling yellow starthistle (*Centaurea solstitialis* L.), although cattle grazing appears to be ineffective

(Hovde 2006). Several studies have shown that repeated grazing can negatively impact spotted knapweed (Olson and Wallander 1997; Olson et al. 1997; Thrift et al. 2008).

Integrated Weed Management. Combining chemical, mechanical, cultural, and biological control methods in an Integrated Weed Management (IWM) approach minimizes inputs and maximizes success in weed control (Hobbs and Humphries 1995). Only in the last decade has carefully managed grazing seriously been considered in IWM strategies on rangeland to accomplish weed control. It is still more common to work grazing management plans around weed control practices than to include grazing in IWM strategies. Shifting weed management strategies to include prescription grazing could increase the efficacy of weed control. Grazing could be combined with chemical or mechanical control measures to improve weed management. Sheep grazing of spotted knapweed was found to be most effective when combined with an herbicide treatment and the combine treatment of herbicide and grazing was more effective than either alone (Sheley et al. 2004). Similarly, Lym et al. (1997) found that, after 3 years of treatment, the combination of herbicide and grazing was better than either treatment alone for Russian (*Rhaponticum repens* [L.] Hidalgo) and spotted knapweed.

Plant Responses to Grazing. Herbivory is one of the most important ecological forces affecting plant communities (Crawley 1983; Huntly 1991; del-Val and Crawley 2005). Many studies confirm that herbivory affects plant community composition (McNaughton 1979; Belsky 1987; Milchunas et al. 1988). Using grazing to control invasive weeds is based on the idea that defoliation of a plant places it at a competitive disadvantage to other plants in the community (Vallentine 1989; Augustine and McNaughton 1998). Plant response to herbivory varies along a continuum from reduced fitness to enhanced growth and reproduction (Maschinski and Witham 1989; del-Val and Crawley 2005). To survive in grazed ecosystems, plants can either reduce the probability or severity of herbivory (called avoidance) or tolerate the damage caused by defoliation (called tolerance; Briske 1996; Juenger and Bergelson 1997; Mauricio et al. 1997).

Avoidance. Avoidance is accomplished by plant attributes that reduce the amount or probability of damage done by an herbivore (Mauricio et al. 1997). Mechanisms for herbivory avoidance include chemical defenses such as alkaloids or tannins, which are toxic or unpalatable to herbivores (Briske 1996), and physical defenses such as dense branching patterns, thorns, or hairy leaf surfaces that can reduce the probability of being grazed or the amount of tissue removed in a defoliation event (Mauricio et al. 1997).

Tolerance. Tolerance is the ability of a plant to sustain a level of tissue damage, without affecting the plant's overall fitness (Painter 1958; Tiffin and Rausher 1999; Mothershead and Marquis 2000). Each plant species has a certain level of tolerance to disturbance and plants vary substantially in how much herbivory they can sustain without causing damage (Hjalten and Danell 1993).

Factors of defoliation. Resource availability, timing, intensity, and frequency of defoliation affect how a plant responds to defoliation (Hochwender et al. 2000; Jameson 1963; McNaughton 1983; Oesterheld and McNaughton 1991). Difficulties in studying the effects of plant response to grazing arise due to the interactions between herbivory, competition, and timing of these processes (Parsons et al. 2007).

Season, Frequency, and Intensity. Seasonal effects of defoliation and general tolerance of defoliation depend upon the species being studied. Grazing yellow starthistle when bolting or earlier results in shorter plants with more buds, whereas grazing after buds began to show on plants resulted in fewer flower heads (Wallace et al. 2008). In the aforementioned del-Val and Crawley (2005) study, all species studied were most sensitive to defoliation when the plants were immature and younger plants were more likely to die with lesser intensities of defoliation. In a broom snakeweed (*Gutierrezia sarothrae* [Pursh] Britton & Rusby) control study, Ralphs and Banks (2009) found that spring grazing resulted in higher seedling establishment, whereas summer grazing resulted in reduced seedlings and juvenile plants. Conversely, long-term studies at the U.S. Sheep Experiment Station in Dubois, Idaho showed greater forb diversity in pastures that were grazed in the fall and lower forb diversity in pastures grazed in the spring (Bork et al. 1998).

Timing of defoliation can also be important in determining plant morphology and structure. Clipping in April did not reduce bluebunch wheatgrass leaf height or biomass in June or July, but clipping in May did affect height and productivity (Brewer et al. 2007). Becklin and Kirkpatrick (2006) found that scarlet gilia (*Ipomopsis aggregata* [Pursh] V.E. Grant ssp. *aggregata*) can compensate for herbivory through both regrowing multiple flower stalks, and by forming ancillary rosettes when grazed in early July. Yellow starthistle had more secondary branching, more buds, and more seeds when grazed early in the year, and shorter plants resulted when grazed in the bolting stage than rosette or late bud stages (Wallace et al. 2008).

The level of intensity of defoliation can profoundly affect plant response to defoliation. Defoliation of a minimum amount of biomass should not affect any plant, but what is normally studied is the level at which defoliation begins to affect the normal growth processes of a plant. In a study of bluebunch wheatgrass, Brewer et al. (2007) found that defoliation to 3 cm reduced both biomass and leaf height, whereas defoliation to 6 cm reduced biomass only.

Few grazing or mowing studies have examined the effects of repeated defoliation on plant response. Rinella et al. (2001) concluded that repeated mowing could decrease spotted knapweed cover and result in a corresponding increase in associated grass cover. However, they also found that a single annual mowing applied in the flowering stage was as effective as repeated mowing.

Community Context. The different reactions of a plant to defoliation also depend on the context in which it is defoliated. If a plant community is a monoculture, with no injection of diversity possible, it may not matter how the community was grazed. For example if an area has no plants other than spotted knapweed, it would not matter the intensity, frequency, or time of grazing; nothing would replace the spotted knapweed. The plant community being studied, along with the reaction of each component of that community to defoliation is of the utmost importance. For example, Rinella et al. (2001) found that mowing decreased spotted knapweed cover to a greater extent than grass cover, therefore mowing appeared to shift the competitive balance in favor of grasses.

It is to no benefit for plant communities if grazing animals do not select for the target plants or eat the plant at a growth stage that is effective for control. Thus, selective herbivory must be considered within the context of the plant community. For example, goats have been shown to eat a greater proportion of leafy spurge when it is grazed in conjunction with arrowleaf balsamroot (*Balsamorhiza sagittata* [Pursh] Nutt.) than with crested wheatgrass wheatgrass (*Agropyron cristatum* L. Gaertn.; Walker et al. 1994).

One approach to using grazing for plant management is to force livestock to consume the target plant by limiting its choices and applying heavy stocking rates. Increasing stocking rates has been shown to cause cattle to graze broom snakeweed enough to reduce its density without adversely affecting crested wheatgrass; (Ralphs and Banks 2009). However, this may not be an option in areas with species more sensitive to grazing, such as bluebunch wheatgrass, which is associated with the plant communities in this study. Another approach is to train grazing animals to graze certain species. This has been successful with goats grazing leafy spurge (Walker et al. 1992) and cattle to grazing broom snakeweed (Ralphs and Wiedmeier 2004). However, diet training procedures are labor intensive and are not a feasible course of action for most livestock operators. A more efficient method is to select animals that naturally will select for the target plant and not the associated plant community, if such an animal is available

Following grazing of the target plant, it is important to note the reaction of the rest of the plant community to the grazing event. Increasing the associated vegetation in a community can increase the negative effect of herbivory on a target plant, therefore it is the inter-specific competition that will keep weed populations low, not the herbivory itself (Crawley 1983; McEvoy et al. 1993; Gurevitch et al. 2000; Parsons et al. 2007).

Competition, coupled with a reduced ability of the defoliated plants to acquire resources can reduce its productivity through reduced root biomass and growth (Gurevitch et al. 2000; Kennett et al. 1992). Fowler and Raucher (1985) evaluated how clipping and density affected the target plant Texas Dutchman's pipe (*Aristolochia reticulata* Jacq.) by clipping the competing species little bluestem (*Schizachyrium scoparium* Michx.) and southern dewberry (*Rubus trivialis* Michx.) or the target plant at varying densities. They found that the presence of competing species reduced the root, shoot, and reproductive mass of the target plant, and the competing grasses had a lesser effect on Texas Dutchman's pipe when they were clipped.

Examining the Role of Defoliation in a Spotted Knapweed Community. Research on spotted knapweed management has shown that defoliation through grazing, clipping, and mowing can control spotted knapweed. Some studies have examined the effects of grazing on spotted knapweed. However, few have studied the mechanisms that allow grazing to successfully control spotted knapweed in a community context. Evaluating vegetation responses to selective or non-selective defoliation in a spotted knapweed infested community is required to determine the best means of using grazing to control spotted knapweed.

Selective grazing should be considered within a successful integrated weed management system. The various responses of different species to defoliation must be considered when using grazing as a weed management tool. These responses differ by season and frequency of defoliation, as does the potential selection of a plant species by an herbivore. The efficacy of repeated defoliation in controlling spotted knapweed has not been well studied, and should be quantified, to evaluate and develop control strategies based on targeted defoliation. This study investigates the response of spotted knapweed and the associated vegetation community to defoliation in several phenological stages, as well as repeated defoliation.

The objectives of this study were to examine the response of spotted knapweed basal cover, density, mortality, and flower production and basal cover and density of the associated vegetation to defoliation at various phenological stages and repeated defoliation. Defoliation treatments consisted of defoliating the spotted knapweed only, the associated vegetation only, all vegetation or an unclipped control at the rosette, bolting, or flowering phenology, or a repeated rosette flowering treatment.

CHAPTER II: Materials and Methods

A field study was conducted from 1999 to 2001 in Eastern Idaho. We examined the cover and reproductive responses of spotted knapweed and associated vegetation to a variety of defoliation treatments. Vegetation assessments were conducted in spring and fall of each year of the study.

Study Site. The study was conducted at the U.S.D.A – Agricultural Research Service, U.S. Sheep Experiment Station; 10 km north of Dubois, Idaho (Figure 2.1). Elevation of the study area was about 1700 m with level to rolling topography and shallow soils with lava outcrops. Soils were mixtures of wind-blown loess, residuum, or alluvium dominated by fine-loamy, mixed, frigid, Calcic Argixerolls (NRCS 1995). The study sites were located on uplands of south to west aspect, and slopes ranged from 0 to 3%.

This is a semiarid region characterized by cold winters and warm summers. Average annual temperature is 6.2^{o} C with extreme temperatures of 37.8^{o} C in summer to –31.7^{o} C in winter (NOAA 2009). The long-term average annual precipitation is 304 mm, primarily occurring as winter snow and spring rain (NOAA 2009). The fall of 1999 was drier than the 30-year average, though with a relatively wet spring in 2000 leading up to the study (Figure 2.2). The rest of 2000, 2001, and 2002 were relatively dry. However, 2003 had a cool, wet spring. The spring of 2000 and 2001 were warmer than normal, however the spring of 2002 and 2003 were about average. The summer of 2000, 2001, 2002, and 2003 were also warmer than normal (Figure 2.3).

The research site was characterized by an over-story of antelope bitterbrush (*Purshia tridentata* [Pursh.] DC.), threetip sagebrush (*Artemisia tripartita* Rydb.), yellow rabbitbrush

(*Chrysothamnus viscidiflorus* [Hook] Nutt.), and spineless horsebrush (*Tetradymia cansescens* DC.). Forbs present in the understory included spotted knapweed, arrowleaf balsamroot, tapertip hawksbeard (*Crepis acuminata* Nutt.), long-leafed phlox (*Phlox longifolia* Nutt.), Hood's phlox (*P. hoodii* Richardson), and granite prickly phlox (*Leptodactylon pungens* [Torr.] J.M. Porter & L.A. Johnson). Native grasses present on the research area were bluebunch wheatgrass, thickspike wheatgrass (*Elymus lanceolatus* [Scribn. & J.G. Sm.] Gould), Indian ricegrass (*Achnatherum hymenoides* [Roemer & J.A. Schultes] Barkworth), needle-and-thread (*Hesperostipatipa comata* [Trin. & Rupr.] Barkworth), Sandberg bluegrass (*Poa secunda* J. Presl.), and prairie junegrass (*Koeleria macrantha* [Ledeb.] J.A. Schultes). The dominant species in each vegetation class were antelope bitterbrush, spotted knapweed, and bluebunch wheatgrass for shrubs, forbs, and grasses, respectively. The vegetative cover, based on canopy cover, on the study sites, averaged 15% shrubs, 5% native forbs, 20% spotted knapweed, and 15% grasses, with 45% bare ground, based on preliminary vegetation assessments of the site.

The research was conducted on three sites within a 2-kilometer radius (Figure 2.3). Two blocks of Site 1 were established in spring 1999 and an additional block of Site 1 and Sites 2 and 3 were established in spring 2000. Site 1 was located in an area commonly used as an overnight resting ground for trailing livestock herds to and from summer range in the spring and fall. Site 2 was commonly grazed by cattle in late spring. Site 3 was a rockier site than the other two sites and was primarily used to graze bulls in the summer before this research project was established. Each study site was fenced using either a four-strand electric fence or a five-strand smooth high-tensile wire fence.

Treatment Applications. Three blocks of treatments were located within each of the three sites. Each block contained 64 (0.1 m^2) plots that were permanently marked on opposite sides with 1-inch PVC pipe and a red #16 nail inserted to ground level. The sampling frame was marked in two places with permanent paint that was aligned with the plot markers to ensure the frame was located in the same spot for each measurement. The dominant spotted knapweed plants in each plot were also marked with a red nail and tracked throughout the study to determine mortality rates. Criteria for choosing a plot were: 1) each plot contained one to two mature spotted knapweed plants; 2) plot centers were greater than 1 meter apart; 3) plots contained 25% shrub cover or less; and, 4) plots contained at least 25% aerial herbaceous cover.

Each plot within a block was randomly assigned a treatment. The study was a factorial arrangement of four levels of defoliation at four times during the growing season on three different sites. The defoliation treatments were: 1) defoliation of spotted knapweed only (Knapweed); 2) defoliation of all herbaceous vegetation including spotted knapweed (All); 3) defoliation of all herbaceous vegetation except knapweed (Other); or 4) a non-defoliated control (Control). The vegetation was defoliated to a stubble height of 3 cm to approximate the grazing height of sheep.

The defoliation treatments were applied at four times during the growing season to create a timing treatment. The timing treatments were: 1) defoliation when spotted knapweed plants were in a rosette stage; 2) defoliation when the knapweed plants were bolting; 3) defoliation when the knapweed plants were in the flowering stage; or 4) defoliation both at the rosette and at the flowering stages. The defoliation treatment was applied to an area of 0.2 m^2 centered on each plot.

Vegetation measurements. Cover and density of plants were estimated before and after the application of treatments. The shrub canopy cover was also estimated. In addition, the total number and basal cover of perennial and annual grasses, perennial and annual forbs, and spotted knapweed of each plot were measured and recorded in the spring and fall. Basal cover was obtained by measuring the circumference of each plant and converting it to area, assuming that the base of each plant was a circle. Total numbers of spotted knapweed flowers per plot were also counted during the flowering period and divided by the number of spotted knapweed plants present to determine the average number of flowers per plant.

Data Analysis. The study was analyzed as a randomized complete block design with a factorial arrangement of treatments. Statistical analyses were made for all aspects of the study using mixed procedures from SAS statistical packages (SAS 2000). Data other than spotted knapweed basal cover were normalized using a log (n+1) transformation for normality. Initial measurements of spotted knapweed basal cover exhibited substantial variability, therefore the change in cover was analyzed. Mean comparisons were conducted using adjusted Tukey's with a significance level of $p<0.1$.

Table 2.1. Pre-Treatment density (mean with standard error) of major life forms measured in three spotted knapweed dominated sites located in Eastern Idaho.

	Study Site							
	1		2		3		Study Average	
Life Form	Density	Std. Err.	Density	Std. Err.	Density	Std. Err.	Density	Std. Err.
Spotted Knapweed	53	± 2.8	51	± 3.1	32	± 2.4	27	± 1.7
Perennial Grass	14	± 8.2	117	± 6.1	162	± 7.4	79	± 4.2
Perennial Forbs	22	± 1.8	16	± 1.5	27	± 2.8	13	± 1.2
Annual Grass	41	± 4.8	6	± 1.8	9	± 2.2	11	± 1.5
Annual Forbs	91	± 6.4	25	± 6.6	55	± 4.1	34	± 4.0

Table 2.2. Pre-treatment basal cover (mean with standard error) of major life forms measured in three spotted knapweed-dominated sites located in Eastern Idaho.

	Study Site							
	1		2		3		Study Average	
Life Form	Cover	Std. Err.	Cover	Std. Err.	Cover	Std. Err.	Cover	Std. Err.
Spotted Knapweed	0.96%	± 0.08%	0.34%	± 0.03%	0.28%	± 0.03%	0.54%	± 0.06%
Perennial Grass	8.41%	± 0.40%	9.34%	± 0.31%	3.87%	± 0.32%	7.30%	± 0.46%
Perennial Forbs	0.03%	± 0.01%	0.07%	± 0.01%	0.06%	± 0.01%	0.06%	± 0.01%
Annual Grass	0.11%	± 0.01%	0.01%	± 0.00%	0.02%	± 0.00%	0.05%	± 0.01%
Total Grass	8.45%	± 0.40%	9.26%	± 0.31%	3.89%	± 0.32%	7.29%	± 0.46%
Annual Forbs	0.13%	± 0.01%	0.05%	± 0.01%	0.11%	± 0.01%	0.10%	± 0.01%

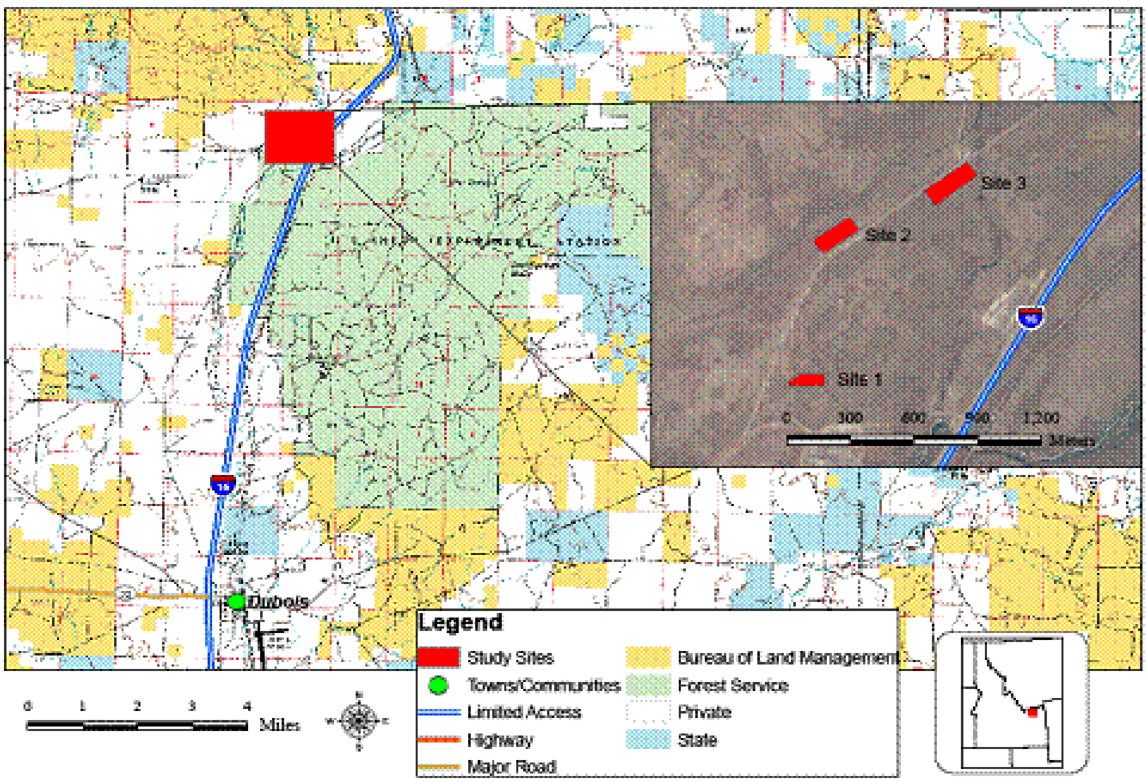

Figure 2.1. Location of research area north of Dubois, Idaho. Three sites were located within a 2 kilometer radius of each other and existed on sites of similar soils and topography.

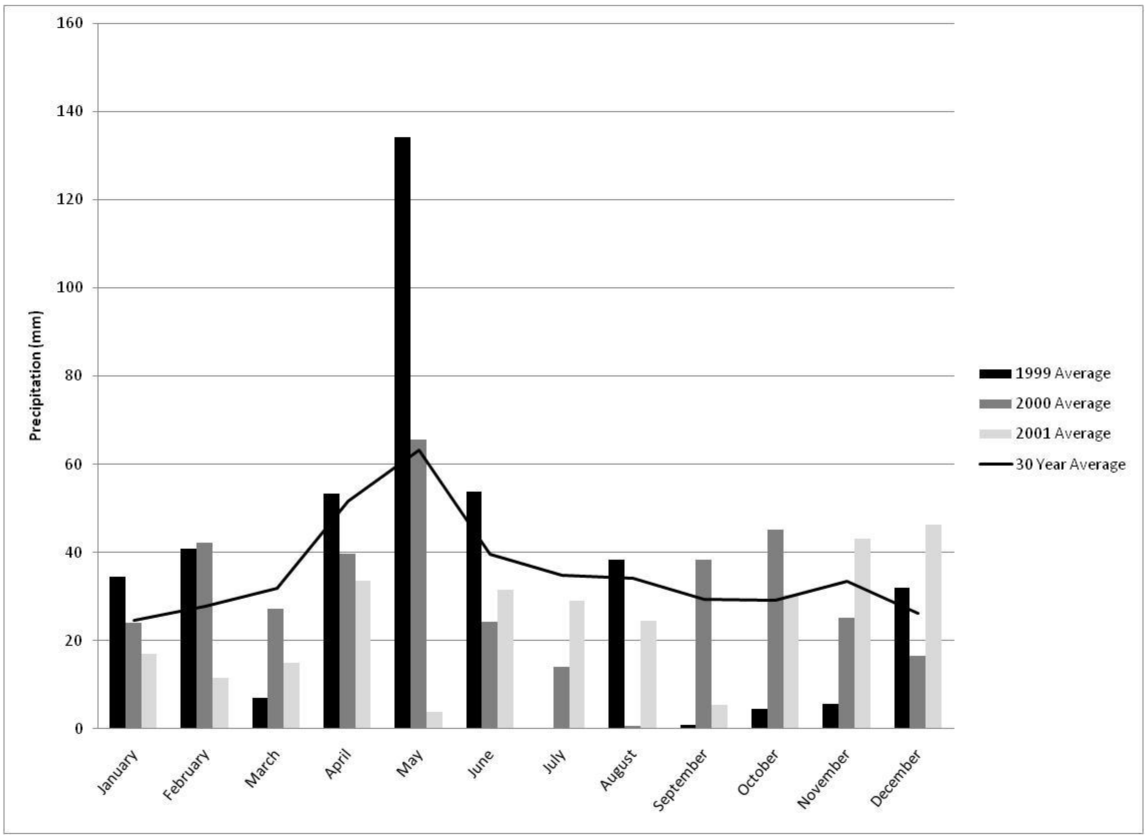

Figure 2.2. Monthly average temperature over the three years affecting the study and the thirty-year average temperature at the United States Sheep Experiment Station in Dubois, ID

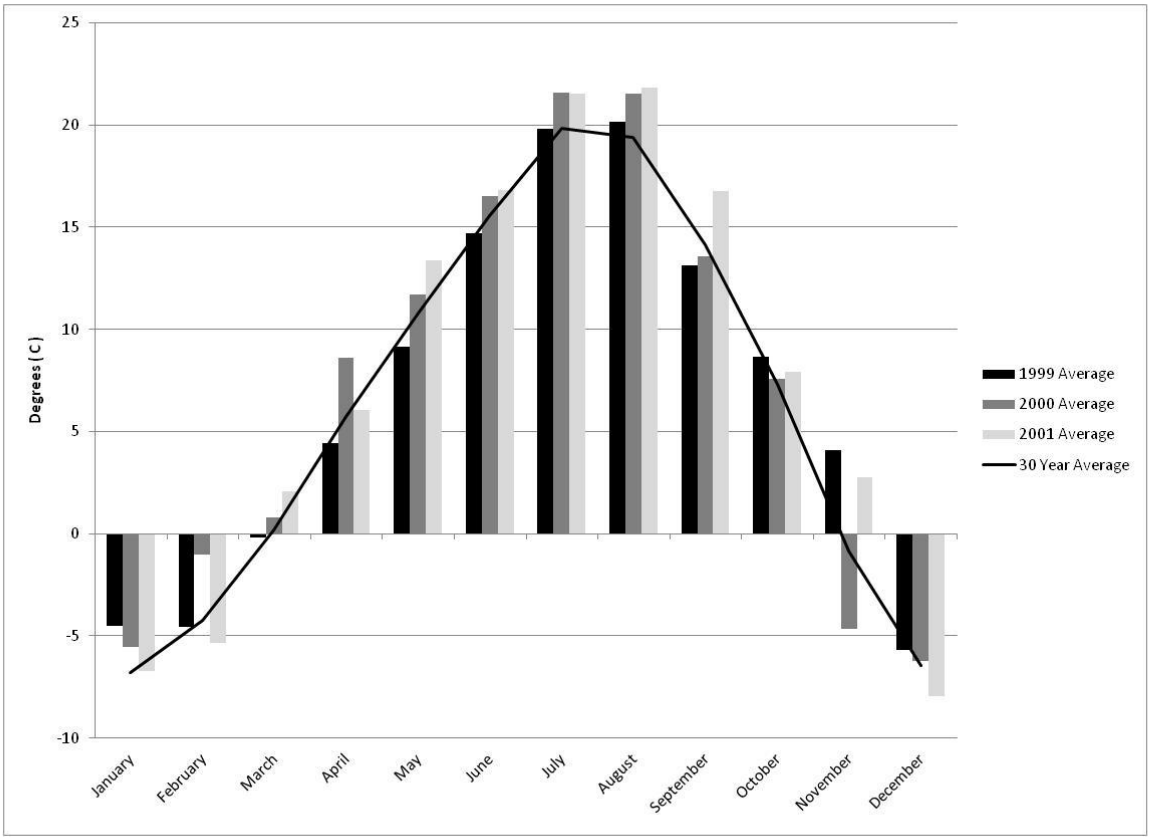

Figure 2.3. Monthly average temperature over the three years affecting the study and the thirty-year average precipitation at the United States Sheep Experiment Station in Dubois, ID.

Chapter III: Results

Spotted Knapweed Mortality. The specific plants tracked throughout the study showed that defoliation generally killed spotted knapweed (Figure 3.1). Greater spotted knapweed mortality occurred when it was clipped (Knapweed and All) than when it was not (Other and Control; $p<0.01$).

The timing of defoliation affected spotted knapweed mortality ($p<0.01$; Figure 3.2). When defoliation occurred in the rosette stage or the repeated defoliation treatment, greater spotted knapweed mortality occurred than in the bolting or flowering stages.

Spotted Knapweed Cover. Substantial variation in spotted knapweed basal area existed in experimental plots before treatments were applied. Therefore, change in cover over the course of the study (i.e., final - initial cover) was analyzed to examine the effects of defoliation on spotted knapweed cover. Spotted knapweed cover increased or decreased during the study depended on the clipping treatment applied ($p=0.01$; Figure 3.3). Cover increased less or decreased when spotted knapweed was clipped (All and Knapweed treatments, respectively) and increased more when it was not clipped (Other and Control treatments). The season at which the defoliation treatment was applied, including repeated defoliation, did not influence change in spotted knapweed cover ($p=0.77$).

Spotted Knapweed Flowers. On all sites, spotted knapweed produced fewer flowers when it was clipped (Knapweed and All treatments) than if it was left unclipped (Other and Control treatments; Figure 3.4). There was a site by defoliation treatment interaction ($p<0.01$), therefore flower production was analyzed by site. This interaction was caused by greater flower production in the Other defoliation treatment on Site 1 compared to the control (p=0.06), but no differences between control and other treatments on the other two sites. As with spotted knapweed cover, season of defoliation did not affect flower production (p>0.1).

Spotted Knapweed Density. Spotted knapweed density expressed a 3-way (site by clip by timing) interaction (p=0.05). Therefore, spotted knapweed density was analyzed by site (Figure 3.5). On sites 1 and 2, spotted knapweed density showed no response to defoliation treatment (p=0.55 site 1; p=0.25 site 2) at any time of treatment (p=0.68 site 1; p=0.75 site 2; Figure 3.5a, b).

On site 3, spotted knapweed density had a defoliation treatment by timing of treatment interaction (p=0.05; Figure 3.5c) and so spotted knapweed density was analyzed by time of defoliation. No effects of clipping treatment were revealed when treatments were examined by timing of treatments. There was only a marginally significant affect of clipping treatment in the repeated treatment (p=0.06).

Perennial Grass Density. Perennial grass density varied by site (p=0.02; Figure 3.6a). Site 3 had greater perennial grass density than the other sites (p=0.02 compared to site 1; p=0.05 compared to site 2). The shallower, rockier soil in site 3 led to a higher density of smaller bunchgrasses. Sites 1 and 2 had similar perennial grass density (p=0.82). Perennial grass density was not affected by defoliation treatment (p=0.56) or timing of defoliation (p=0.95).

Perennial Grass Cover. Perennial grass cover was lower on site 3 than the other sites (p=0.01; Figure 3.6b) prior to initiating the study. Site 3 was a less productive site overall, due to rocky, shallow soils. Neither the defoliation treatment ($p=0.56$) nor the timing of defoliation ($p=0.78$) affected perennial grass cover.

Perennial Forb Density. There was a site by defoliation treatment interaction for perennial forb density ($p=0.04$), so sites were analyzed separately. On site 1, neither defoliation treatment ($p=0.87$) nor the timing of defoliation ($p=0.87$) affected perennial forb density (Figure 3.7). On site 2, perennial forb density was affected by defoliation treatment ($p<0.01$) and the timing of defoliation ($p=0.02$; Figure 3.8). Greater perennial forb density occurred on site 2 when perennial forbs were not clipped (i.e., Control and Knapweed treatments) than when other vegetation was clipped. When all vegetation was clipped on that site, perennial forb density was lower than the control, but similar to other treatments. Neither defoliation treatment ($p=0.93$) nor the timing of defoliation ($p=0.59$) affected perennial forb density on site 3.

However, once analyzed by site, timing differences arose on site 2 ($p=0.02$; Figure 3.9); perennial forb density was greater if defoliation occurred at the flowering stage of spotted knapweed than any other time, no matter the defoliation treatment.

Perennial Forb Cover. Perennial forb cover was higher on site 2 than site 1 ($p=0.06$), regardless of treatment applied (Figure 3.10). Site three was similar to both site 1 ($p=0.88$) and site 2 ($p=0.12$). Neither the defoliation treatment ($p=0.15$) nor the timing of defoliation ($p=0.17$) affected perennial forb cover.

Annual Grass Density and Cover. Both annual grass cover and density differed by site (cover p=0.01; density p<0.01; Figure 3.11). Annual grass cover and density were highest on site 1 and similar on sites 2 and 3. Defoliation treatments affected cover and density in similar ways (cover p=0.01; density p=0.02) on all three sites (i.e., there was no site by defoliation interaction; cover p=0.11, density p=0.19). The knapweed clipped treatment resulted in higher annual grass cover (p<0.01; Figure 3.11) and density (p=0.02) than when all vegetation was clipped with intermediate values for other defoliation treatments.

Annual Forb Density and Cover. Both annual forb density and cover differed by site (density p=0.03; cover p=0.06; Figure 3.12). Annual forb cover and density were highest on site 1, lowest on site 2, and intermediate on site 3 (i.e., site 3 was similar to sites 1 and 2). Neither defoliation treatment, nor the time at which defoliation occurred affected annual forb density (0.43 and 0.24, respectively).

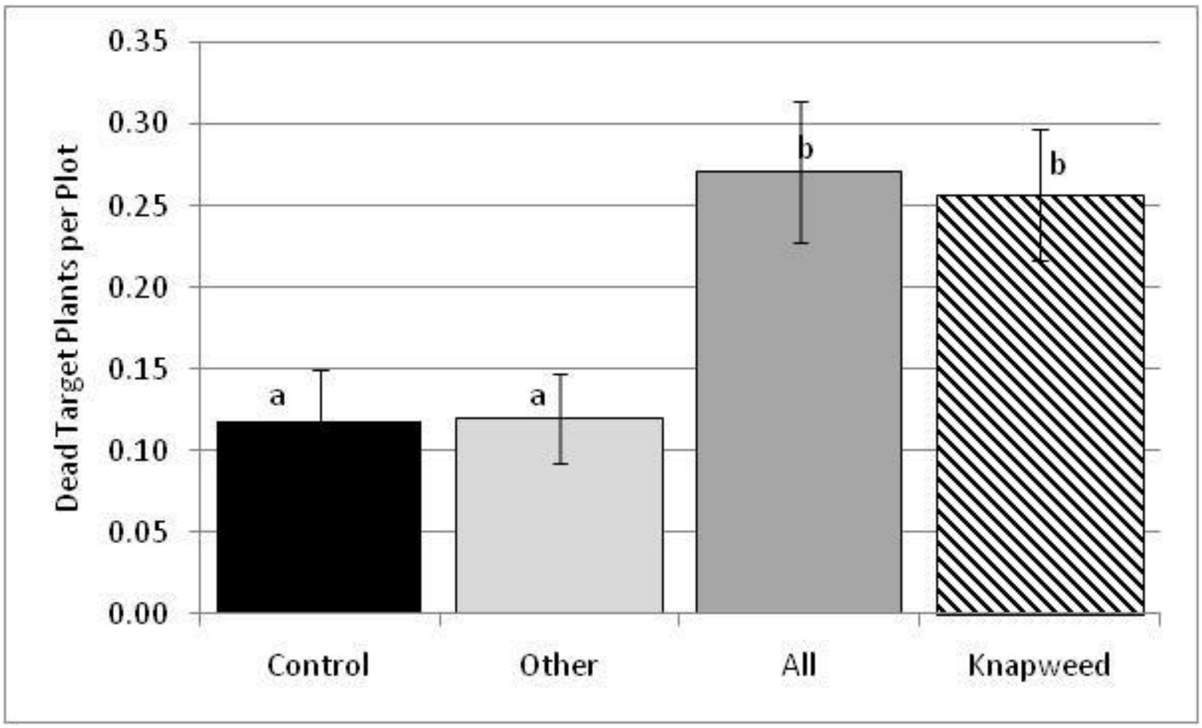

Figure 3.1. Average number of dead target plants per plot in each clipping treatment at the end of the study (Fall 2001) with standard error bars. Treatments with no significant differences are indicated with the same letter at the top of the bar.

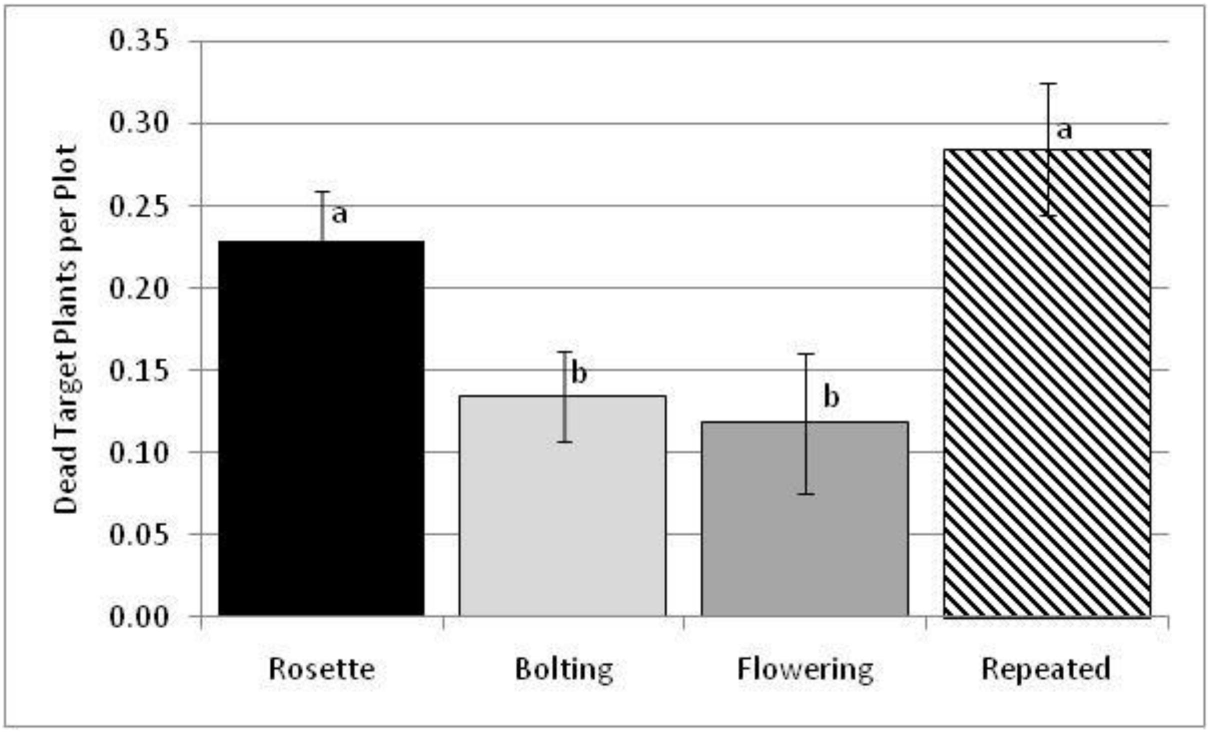

Figure 3.2. Average number of dead target plants per plot in each phenology treatment at the end of the study (Fall 2001) with standard error bars. Treatments with no significant differences are indicated with the same letter at the top of the bar.

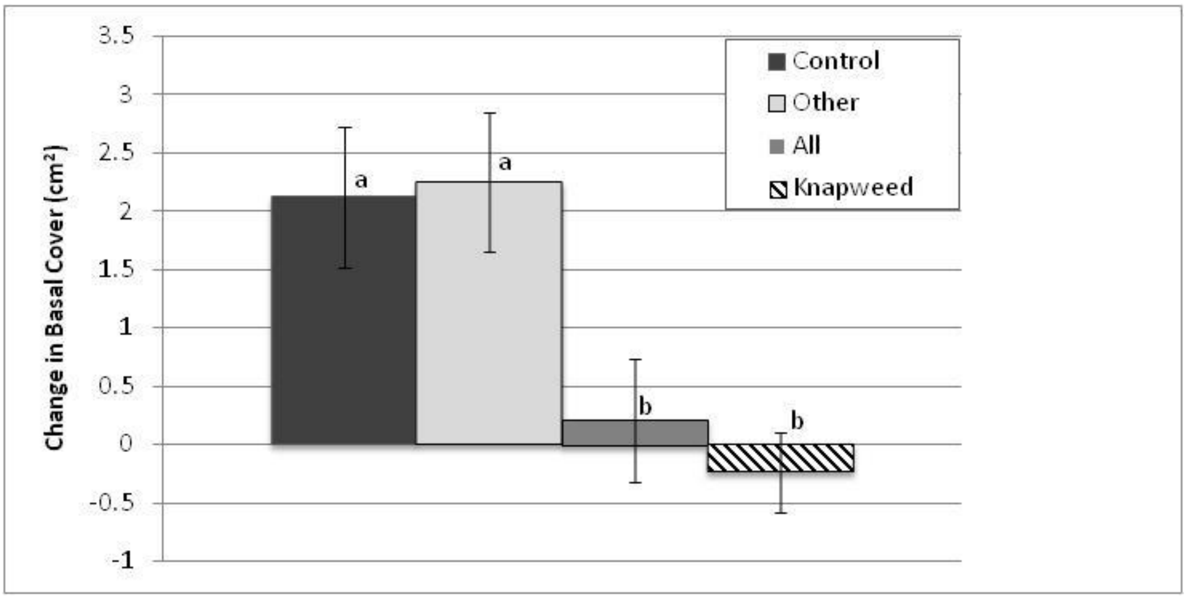

Figure 3.3. Change in basal area (post-treatment minus pre-treatment) of spotted knapweed plants in each clipping treatment with standard error bars. Treatments with no significant differences are indicated with the same letter at the top of the bar.

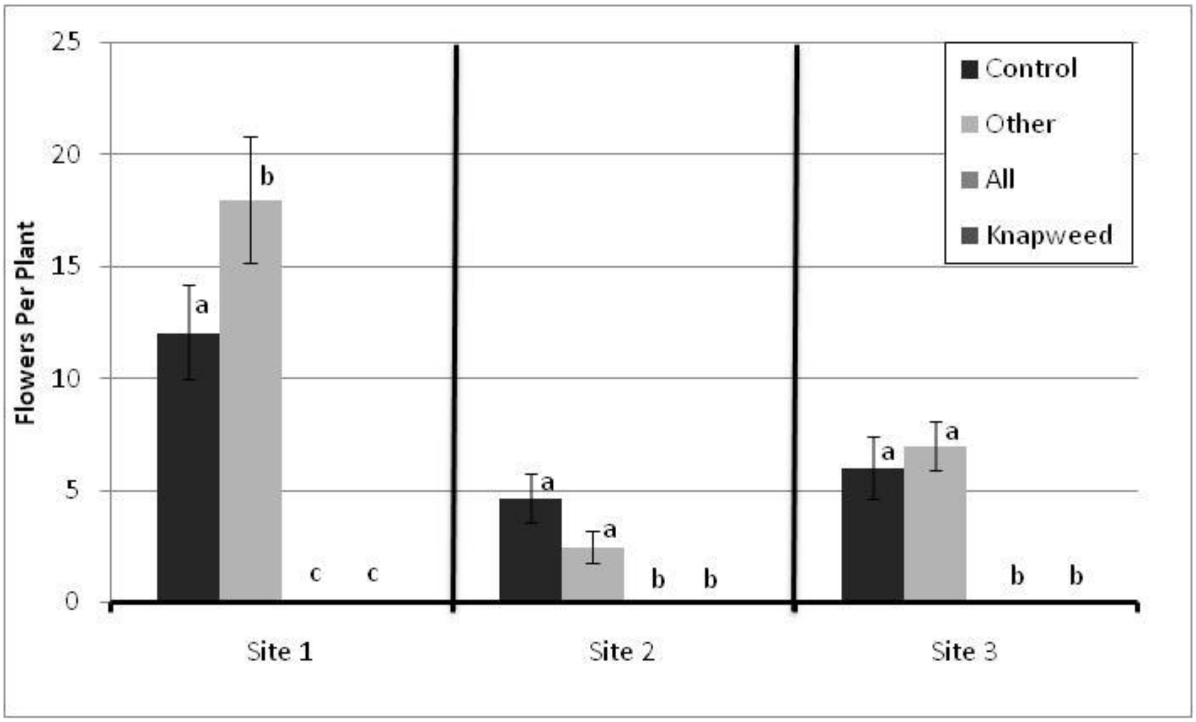

Figure 3.4. Average number of spotted knapweed flowers per plant in each clipping treatment on Sites 1, 2, and 3 with standard error bars. Treatments with no significant differences are indicated with the same letter at the top of the bar.

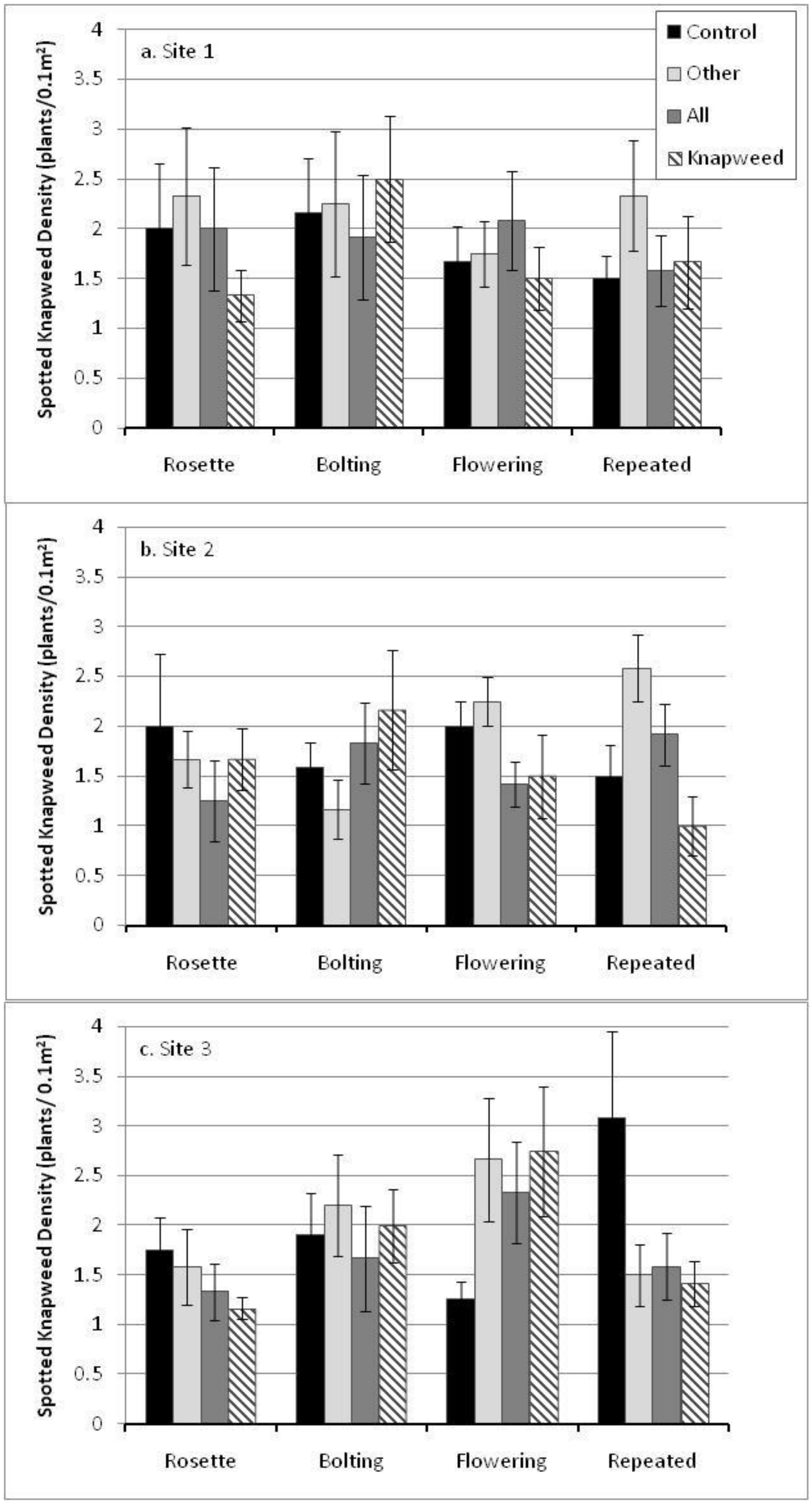

Figure 3.5. Spotted knapweed density as affected by clipping and phenology treatment on Sites 1 (a), 2 (b), and 3 (c) with standard error bars.

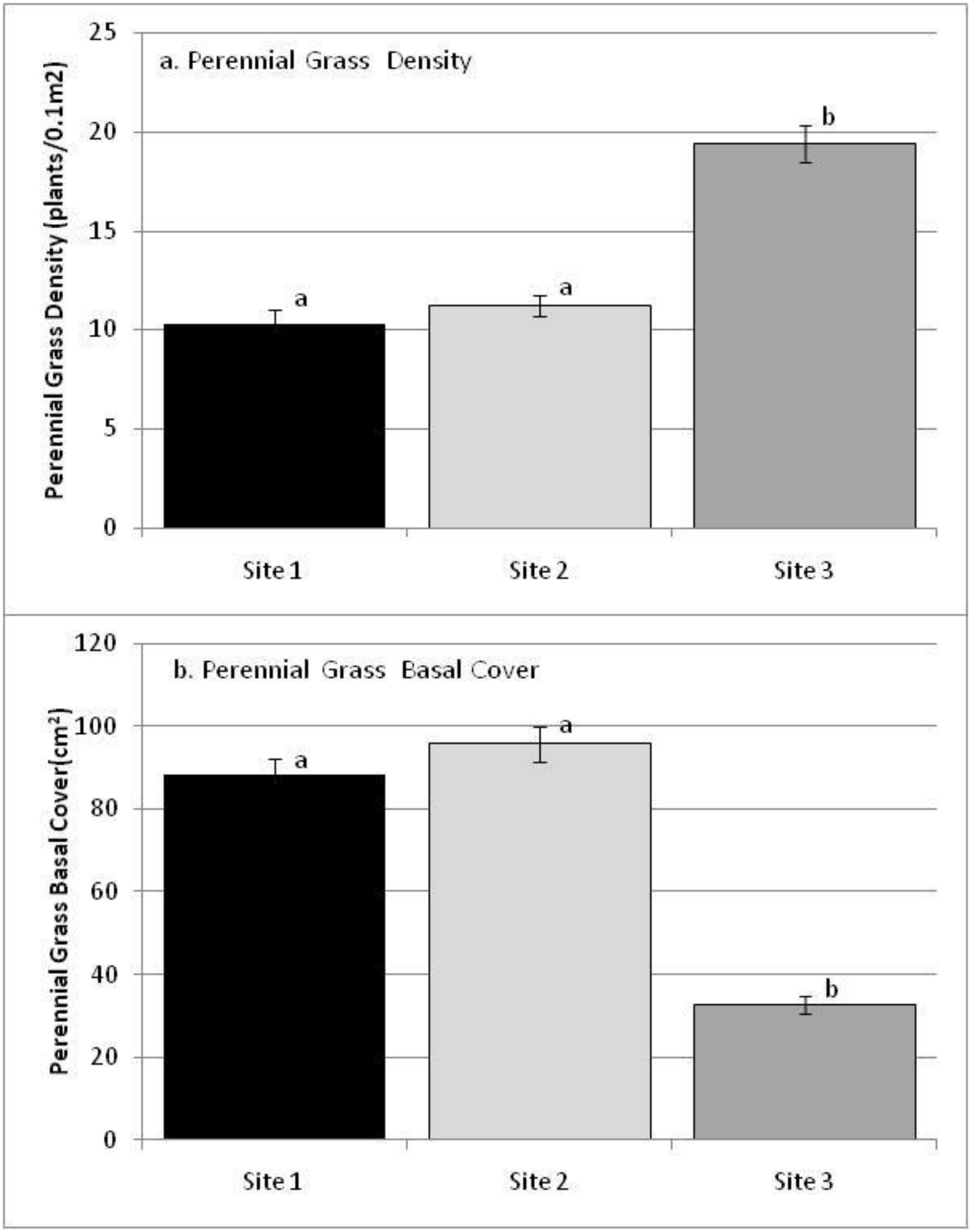

Figure 3.6. Perennial grass density (a) and basal cover (b) on Sites 1, 2, and 3 with standard error bars. Treatments with no significant differences are indicated with the same letter at the top of the bar.

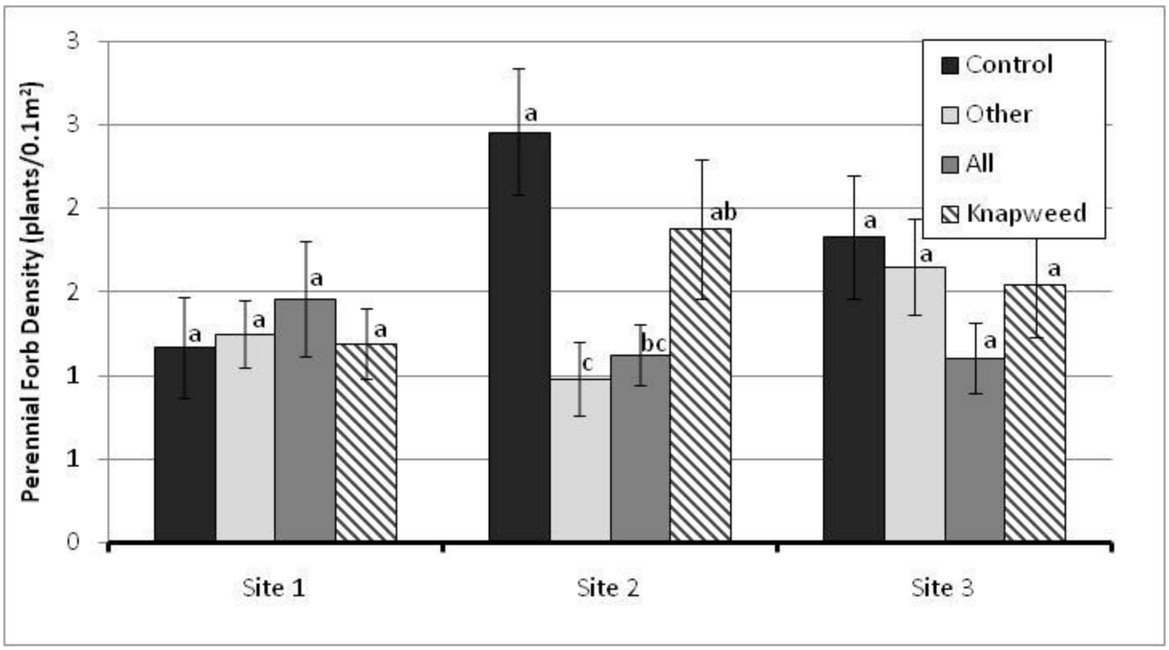

Figure 3.7. Perennial forb density as affected by clipping treatment on Sites 1, 2, and 3 with standard error bars. Treatments with no significant differences are indicated with the same letter at the top of the bar.

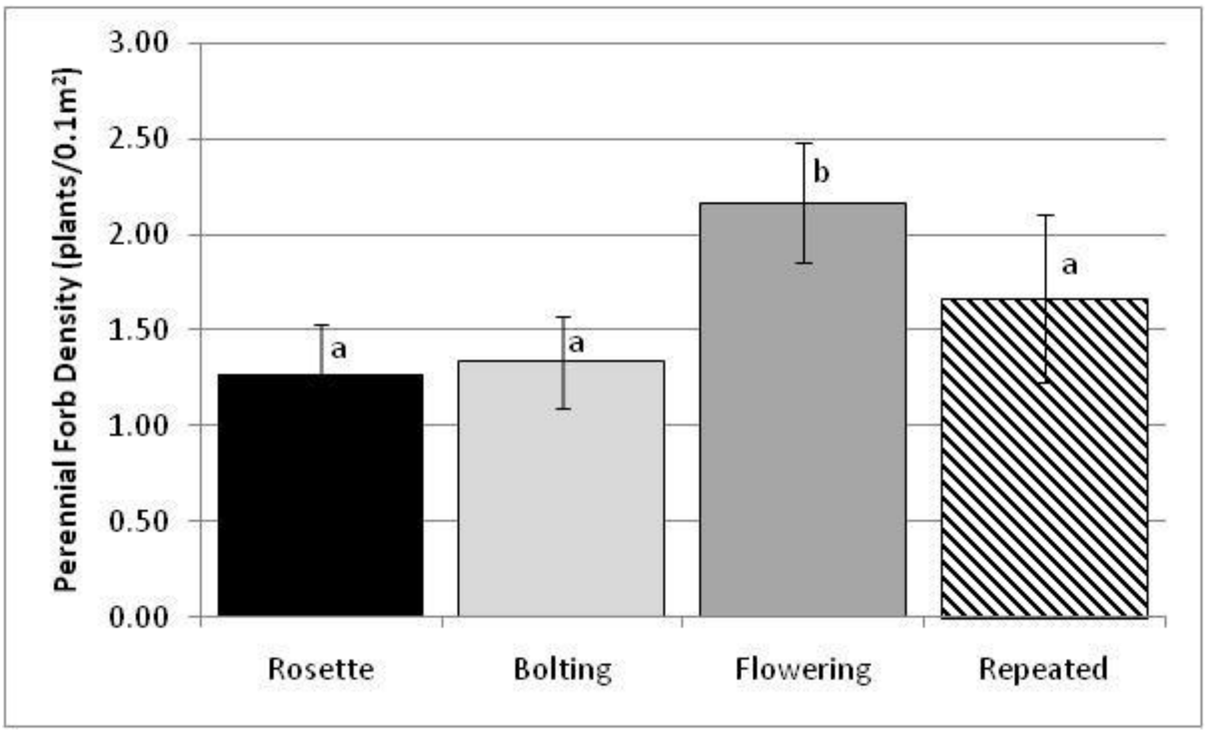

Figure 3.8. Perennial forb density on Site 2 as affected by timing of clipping treatment with standard error bars. Treatments with no significant differences are indicated with the same letter at the top of the bar.

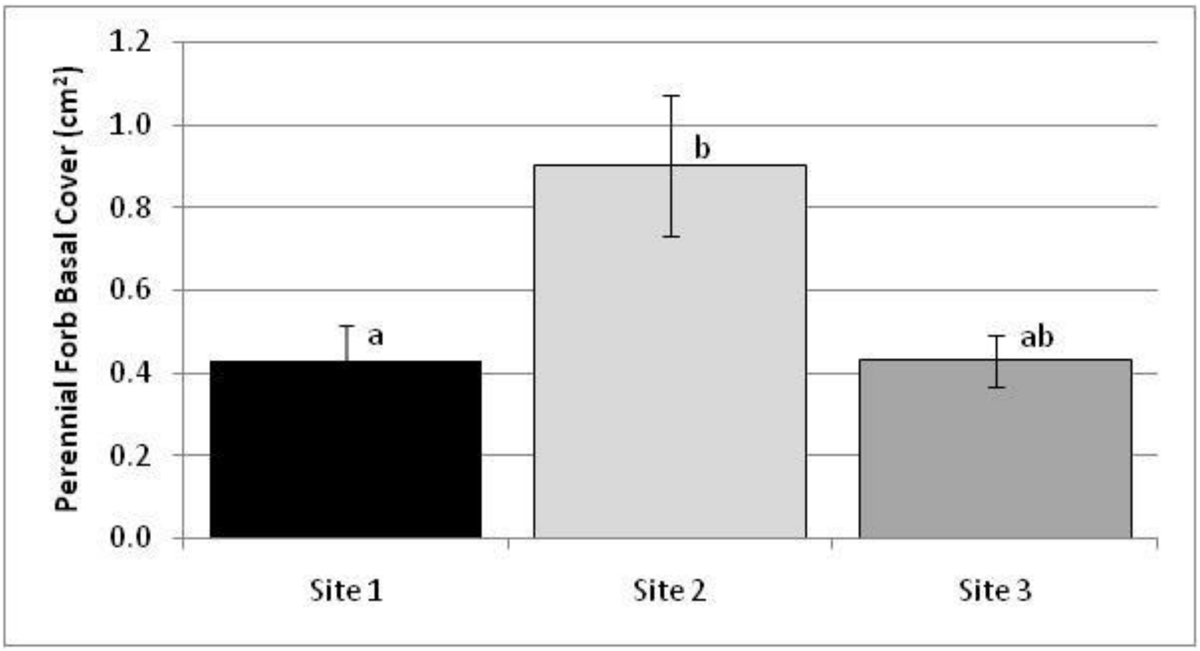

Figure 3.9. Perennial forb basal cover on Sites 1, 2, and 3 with standard error bars. Treatments with no significant differences are indicated with the same letter at the top of the bar.

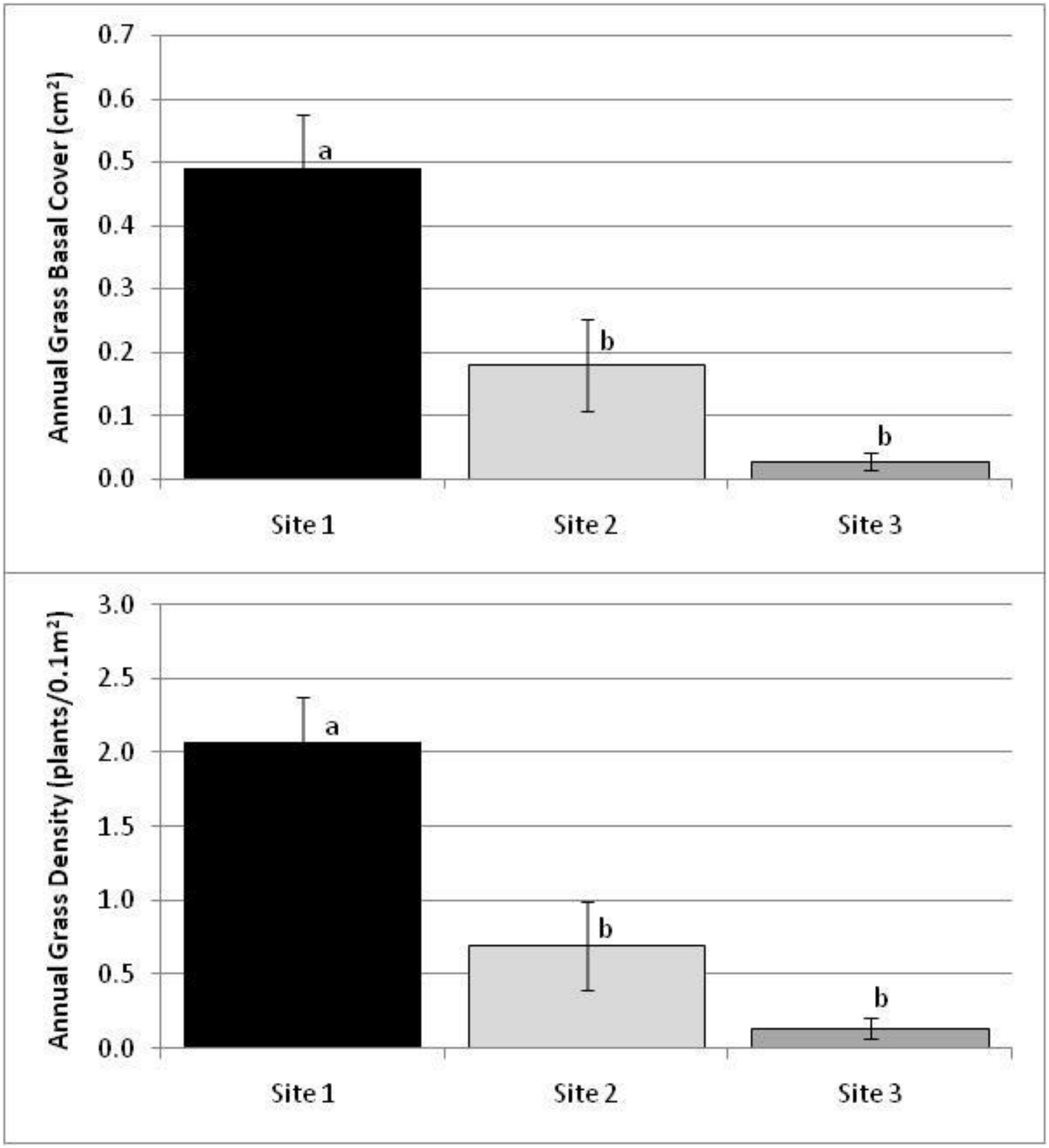

Figure 3.10. Annual grass basal cover (a) and density (b) on Sites 1, 2, and 3 with standard error bars. Treatments with no significant differences are indicated with the same letter at the top of the bar.

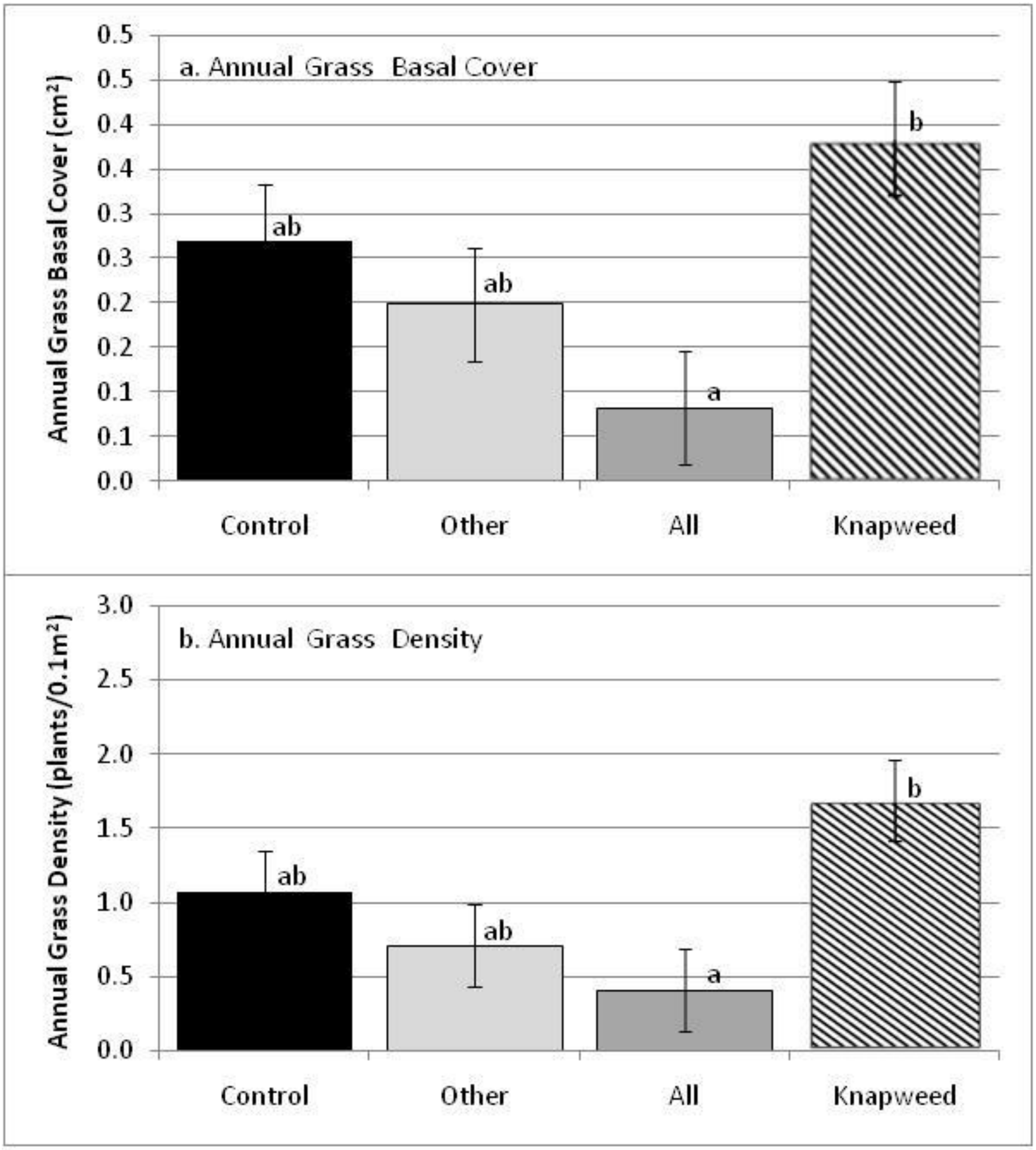

Figure 3.11. Annual grass basal cover (a) and density (b) in each clipping treatment with standard error bars. Treatments with no significant differences are indicated with the same letter at the top of the bar.

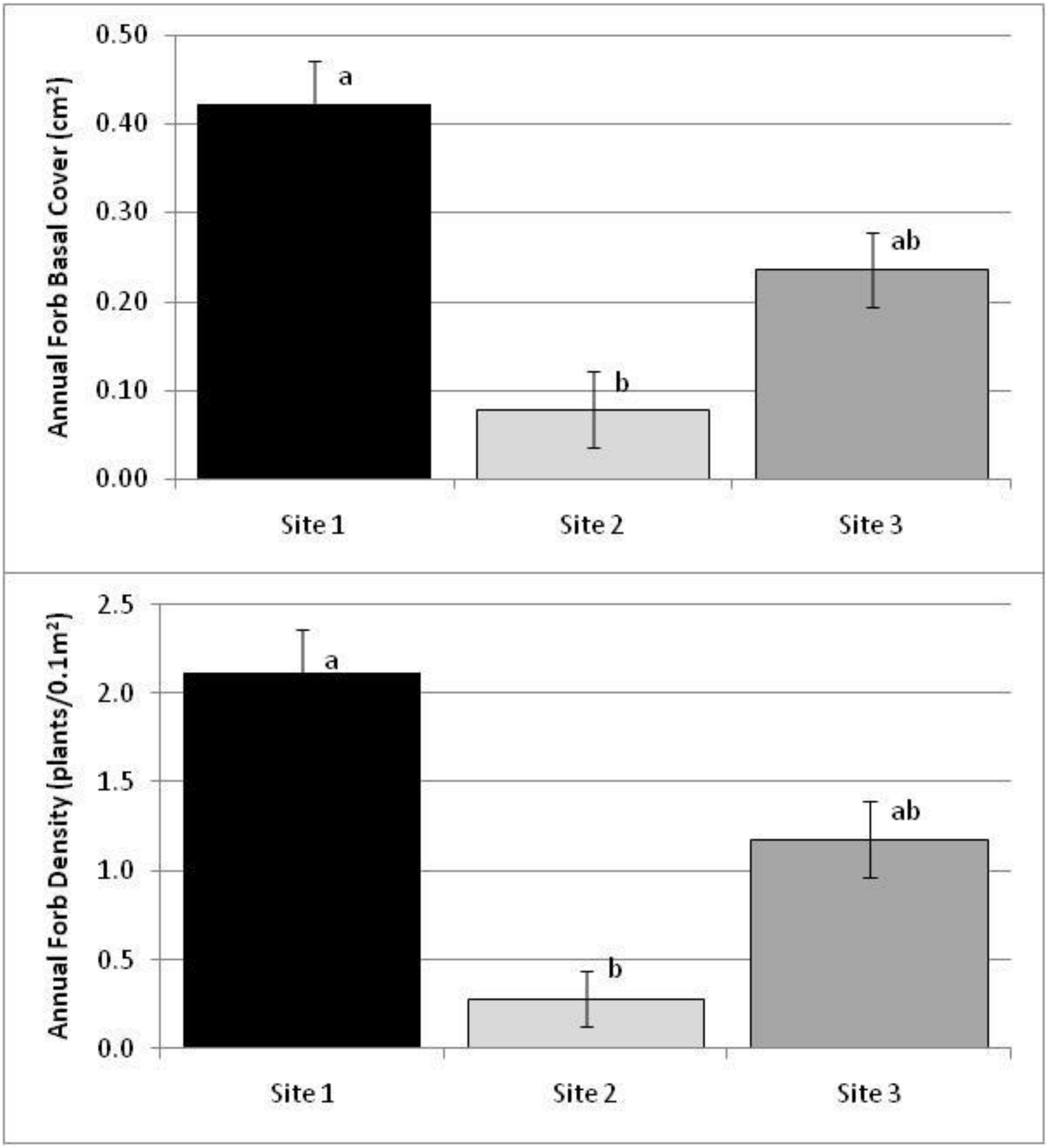

Figure 3.12. Annual forb basal cover (a) and density (b) on Sites 1, 2, and 3 with standard error bars. Treatments with no significant differences are indicated with the same letter at the top of the bar.

Chapter IV: Discussion

The study objectives were to determine whether spotted knapweed and the associated vegetation community were more susceptible to defoliation during certain phenological stages. We evaluated competitive interactions in these communities by examining basal cover and density. Our data indicated that spotted knapweed is susceptible to defoliation throughout the growing season, regardless of whether the associated vegetation was defoliated. We also found that the associated vegetation community was relatively unaffected by defoliation in our study.

Spotted Knapweed Mortality. Defoliation of spotted knapweed was the most important factor in determining individual spotted knapweed mortality. Mortality was unaffected whether the spotted knapweed was defoliated either alone or in conjunction with the associated vegetation, indicating competition had a minor impact on individual plant mortality. This suggests that not only selective grazers such as sheep or goats may impact spotted knapweed, but less selective grazers, such as cattle, or other mechanical treatments, such as mowing, could cause on spotted knapweed mortality. Of the few studies examining spotted knapweed response to defoliation (Jacobs and Sheley 1997 [clipping, greenhouse]; Kennett et al. 1992 [clipping, greenhouse]; Muller et al. 1988 [biocontrol]; Olson and Wallander 2001 [grazing]; Olson et al. 1997 [grazing]; Rinella et al. 2001 [mowing]; Story et al. 1989 [insects]; Story et al. 2008[insects]; Thrift et al. 2008 [grazing]), none have investigated the mortality of individual plants. However we have found that clipping can lead to mortality in purple loosestrife (*Lythrum salicaria* L.; Stamm Katovich et al. 1999).

Defoliation at the rosette phenological stage and repeated defoliation resulted in higher individual spotted knapweed mortality than defoliating at the bolting or flowering phenological stages. This indicates that spotted knapweed was more sensitive to herbivory in the rosette phenological stage than other seasons. One possible explanation is that there were not enough carbohydrate reserves in the root and shoot to replenish leaf area and recover from defoliation. These defoliations were relatively severe, leaving only 3 cm of leaf material above the soil surface, which may not have been enough photosynthetic material to replenish those carbohydrate reserves and regrow. Olson and Wallander (1997) found that grazing reduced shoot carbohydrate reserves but did not affect root carbohydrate reserves.

Spotted Knapweed Cover. Spotted knapweed cover was affected by defoliation treatment such that lower cover resulted when knapweed was clipped than when it was not. Many studies show that defoliation can reduce the biomass of plants. Defoliation can limit a plant's ability to compete for and store resources (Gurevitch et al. 2000).

Unlike observations on plant mortality, the timing of defoliation does not appear to be a factor in reducing spotted knapweed cover. This could be the result of either newly established rosettes after defoliation of the plots or compensation by those rosettes that remain. Though greater mortality occurred when spotted knapweed was defoliated at the rosette phenology, rosettes that became established after the clipping treatment could result in no net differences in cover at the end of the season. Cover of rosettes established after the clipping treatment or increases in cover of surviving plants resulted in similar cover at the end of the season, regardless of timing of defoliation.

Spotted Knapweed Flowers. Spotted knapweed flower production was highly influenced by clipping treatment with lower flower production resulting when spotted knapweed was clipped. This indicates that one or more resources were limited enough that spotted knapweed was unable to recover from defoliation. One reason may have been due to interspecific competition for moisture during the earlier part of the growing season, when grasses were still actively growing. Another possibility is that there was not an adequate amount of growing season left after the later defoliation treatments.

There were however, some differences in the effects of clipping treatment on spotted knapweed flower production between sites. Treatments were initiated one year sooner on Site 1 than on Sites 2 and 3. Earlier treatment initiation and larger spotted knapweed plant size on Site 1 (personal observation), may explain differences between sites in spotted knapweed flower production. Three seasons of defoliating the associated vegetation in Site 1 compared to two seasons for Sites 2 and 3 may have led to a competitive advantage for spotted knapweed, allowing higher flower production in Site 1. These treatments still had higher flower production than the All and Knapweed defoliation treatments, but two years of defoliation may not have been enough to differentiate the Vegetation defoliation treatment and the Control.

Spotted Knapweed Density. Although defoliation influenced spotted knapweed plant mortality and radically reduced flower production and cover, it did not affect density at the plot level. This was due to the establishment of new rosettes throughout the growing season. The influence of grazing on plant density is complicated by the recruitment of new plants after defoliation influencing measurements at the end of the season. This new recruitment is the only reasonable explanation for increases in plant density after defoliation.

Associated Plant Community. Our data indicate that defoliation had little effect on associated vegetation. Perennial grass cover and density in our study were only influenced by site, and not responsive to defoliation treatments. These results agree with work by Rinella et al. (2001), who reported that mowing decreased spotted knapweed cover and density without affecting bluebunch wheatgrass or rough fescue.

Our study showed no defoliation or timing of defoliation effects on perennial forb cover and only one site had defoliation and timing effects on forb density. However, long-term studies at the US Sheep Experiment Station in Dubois, Idaho showed greater forb diversity in pastures that were grazed in the fall and lower forb diversity in pastures grazed in the spring (Bork et al. 1998). The primary perennial forbs on Sites 1 and 3 were phlox species, which have multiple basal stems, would not be greatly affected by defoliation at the 3 centimeter level. Site 2 was somewhat more diverse, but evidently basal cover of those species was also not susceptible to defoliation.

Only Site 2 showed defoliation and timing effects on perennial forb density. Perennial forb density on Site 2 showed similar reactions to defoliation and its timing to those shown by spotted knapweed. Site 2 had greater forb diversity than the other Sites, with larger, more robust species such as arrowleaf balsamroot and tapertip hawksbeard, and these different species may have been less able to recover from defoliation. Perennial forb density also appeared to be less impacted by defoliation when spotted knapweed is in the flowering phenology than at other stages, when considered across defoliation treatments. Bork et al.

(1998) found that large robust species such as arrowleaf balsamroot, fernleaf biscuitroot (*Lomatium dissectum* [Nutt.] Mathias & Constance), and tapertip hawksbeard were less able to recover from spring defoliation than other perennial forbs. This factor should be considered when selecting a control method for spotted knapweed in communities with these types of forbs present.

Regardless of site, when spotted knapweed was defoliated there was higher annual grass cover and density than when all vegetation was defoliated. This result is likely due to the small stature and short longevity of the cheatgrass (*Bromus tectorum* L.) and Japanese brome (*Bromus arvensis* L.) that inhabited the study area. During this study, these annual grasses had generally completed their life cycle even before the rosette defoliation was occurring. Therefore, if it was clipped it was not going to recover, unless there was another flush of moisture and new seed germination (Haferkamp and Karl 1999). The only difference encountered was between the two treatments that involved defoliating spotted knapweed. A completely opened up canopy from defoliating all vegetation could result in a drier microsite at the soil surface, where the majority of the annual grass seed is located, possibly reducing the chances of annual grass seed germination (Cooley and Robertson 1984). If only the spotted knapweed were defoliated, there would still be a slight sheltering from wind and sun, and could result in a more moist microsite, allowing for annual grass seed germination.

Annual forbs were unaffected by defoliation treatments or its timing. Some differences were observed between sites, but as with perennial forb cover differences, these differences were observed on the Sites prior to the study. Several years of defoliation under this regime may affect some changes, but the three years of this study did not alter annual forb density or cover.

Chapter V: Management Implications

Our study showed that defoliating spotted knapweed can result in lower flower production, reduced cover, and death of individual plants. Though it did not reduce overall density in our study, longer periods of defoliation could have the desired effect. If spotted knapweed plants are killed through defoliation, and those that survive produce fewer flowers, defoliation over a period of several years should result in reduced populations and density. The short (3 year duration) of our study did not show reduced density, however, spotted knapweed seed can persist in the soil for up to seven years (Sheley et al. 1998), which would require multiple years of reducing seed input to influence the seed bank.

Spotted knapweed at the rosette and bolting phenology is highly palatable and nutritious to sheep (Ganguli et al. In Press). Though grazing at the rosette phase is damaging to the plant and it is highly nutritious, it does not mean that spring grazing would be the most desirable time for selective grazing. This is because you need to consider the response of the associated vegetation and selectivity of the herbivore.

Our study also showed that defoliation of the associated plant community, rather than spotted knapweed, over longer periods, as was done on Site 1, can yield higher spotted knapweed flower production than other treatments. This indicates that grazers that are less selective in their diet or that select for spotted knapweed would be best suited for controlling spotted knapweed if the community still has the desired vegetation components. Though neither two nor three years of defoliating the associated plant community resulted in any effect, the increased flower production would allow spotted knapweed to spread to other areas at a high rate.

The density of larger, more robust forbs appears more sensitive to defoliation than other perennial forbs. On Site 2, the density of forbs such as tapertip hawksbeard and blue penstemon was reduced when the associated plants were defoliated compared to the knapweed defoliation treatment and control, whereas on Site 3, which had primarily long-leafed phlox as its perennial forb component, perennial forbs were largely unaffected, regardless of defoliation treatment. This was particularly pronounced when defoliation occurred in the flowering phenology treatment. This indicates that these more robust forbs may end up being reduced in efforts to control spotted knapweed through defoliation.

When developing an IPM strategy, the use of grazing animals should be considered. Our data show that defoliation of spotted knapweed can help control the weed, with little effects to the associated vegetation community. Our data also show that less selective grazers, such as cattle and horses could be used to control spotted knapweed. More specialist grazers, such as sheep and goats, could also be used, provided that they select for the weed and do not avoid it.

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Appendix 1: Probability of significance for each parameter measured in a 3-year study of plant response in a spotted knapweed- dominated community in Eastern Idaho.

		Treatment						
Life Form	Parameter	site	clip	site*clip	phen	site *phen	phen *clip	site *phen *clip
Spotted Knapweed	Cover	0.8335	0.0778	0.9311	0.1916	0.6079	0.3315	0.0479
	Density	0.2291	0.0139	0.0845	0.7721	0.5588	0.6944	0.1868
	Flowers	0.0146	0.0000	0.0000	0.0749	0.5352	0.3324	0.4505
	Mortality	0.1233	0.0019	0.6730	0.0026	0.3641	0.3121	0.3963
Perennial Grass	Cover	0.0115	0.5563	0.4780	0.7792	0.4650	0.3439	0.9657
	Density	0.0221	0.5647	0.7513	0.9488	0.6302	0.9022	0.4796
Perennial Forb	Cover	0.0605	0.1506	0.1271	0.1682	0.5455	0.1687	0.3723
	Density	0.4649	0.1485	0.0431	0.1201	0.6656	0.3530	0.5518

Appendix 1: Probability of significance for each parameter measured in a 3-year study of plant response in a spotted knapweed- dominated community in Eastern Idaho.

		Treatment						
Life Form	Parameter	site	clip	site*clip	phen	site *phen	phen *clip	site *phen *clip
Annual Grass	Cover	0.0110	0.0116	0.1110	0.3666	0.5514	0.9618	0.9746
	Density	0.0024	0.0182	0.1929	0.4189	0.6375	0.7648	0.9601
Annual Forb	Cover	0.0691	0.2091	0.8165	0.3336	0.2778	0.2644	0.6223
	Density	0.0328	0.4261	0.8962	0.2354	0.2139	0.3078	0.8991
Total Grass	Cover	0.0109	0.5330	0.4675	0.7977	0.4811	0.3451	0.9648
	Density	0.0506	0.3847	0.8695	0.9986	0.4217	0.8353	0.3021