

EFFECTS OF PERENNIAL PLANT COMPETITION ON THE INVASIBILITY OF
CANYON GRASSLAND COMMUNITIES BY *CENTAUREA SOLSTITIALIS*

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Sandra S. Robins

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Major Professor: Stephen C. Bunting, Ph.D.

AUTHORIZATION TO SUBMIT

THESIS

This thesis of Sandra S. Robins, submitted for the degree of Master of Science with a major in Range Resources, and titled “ Effects of Perennial Plant Competition on the Invasibility of Canyon Grassland Communities by *Centaurea solstitialis*”, has been reviewed in final form. Permission, as indicated by the signatures and dates given below, is now granted to submit final copies to the College of Graduate Studies for approval.

Major Professor _____ Date _____
 Stephen C. Bunting

Committee
 Members _____ Date _____
 James L. Kingery

_____ Date _____
 Timothy S. Prather

Department
 Administrator _____ Date _____
 Kendall L. Johnson

College Dean _____ Date _____
 Leonard R. Johnson

Final Approval and Acceptance by the College of Graduate Studies

_____ Date _____
 Charles R. Hatch

ABSTRACT

Centaurea solstitialis poses a serious threat to canyon grassland communities in the western United States. Invasibility of canyon grasslands has been correlated with low levels of plant cover, indicating plant competition is an important factor of invasibility. The objective of this study is to determine if a threshold for invasibility exists along the successional gradient of a *Pseudoroegneria spicata* (bluebunch wheatgrass)/*Poa secunda* (Sandberg bluegrass) habitat type.

Sites along the successional gradient varying from early seral annual dominated communities to late seral perennial dominated communities were assessed for their susceptibility to *Centaurea solstitialis* invasion. Plant competition was inferred by perennial plant percent cover. Competition from perennial grasses and cryptogams appears to be a limiting factor for success of *Centaurea solstitialis* invasion. A threshold was shown to exist along the successional gradient at a 10 to 15% cover level on moderate (15 to 60%) slopes. Above this abundance level *Centaurea solstitialis* densities remain low, suggesting established perennial grass cover as low as 10 to 15% may be sufficient to resist invasion.

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INTRODUCTION

The canyon grasslands of northwestern Idaho, southeastern Washington and northeastern Oregon historically have experienced a sequence of biological invasions by invasive plant species. Invasions by *Bromus tectorum* (cheatgrass), *Hypericum perforatum* (St. John's wort), *Taeniatherum caput-medusae* (medusahead), and recently, *Centaurea solstitialis* (yellow starthistle) have had significant effects on the composition and function of these grasslands (Tisdale 1986). Weed control efforts have been partially successful in controlling some invasive species. However, plant communities within the canyon grassland ecosystem appear to be highly susceptible to invasion by successive invasive species each time control of one invading species is achieved.

Weed management efforts often focus on simply controlling weeds, with limited regard to the existing or resulting plant community (Jacobs et al. 1999). Weed control, while important, addresses the symptoms rather than the apparent high invasibility of canyon grasslands. Identifying site-specific aspects of a habitat's condition may further develop our understanding of what makes it susceptible to invasion by species such as *C. solstitialis*.

Identification of perennial plant competitive ability and site disturbance may help explain the invasibility of grassland communities. The goal of this research was to determine if a threshold exists for invasibility by *C. solstitialis* along the successional gradient of a *Pseudoroegneria spicata* (bluebunch wheatgrass)/*Poa secunda* (Sandberg bluegrass) grassland habitat type. Selected sites of this habitat type were assessed for their susceptibility to *C. solstitialis* invasion. Comparisons were made along the successional gradient varying from annual dominated communities (early seral) to those dominated by perennial plants (late seral) within the *Pseudoroegneria spicata*/*Poa secunda* habitat type.

The threshold in this study is defined as the zone of division between the rate of change of *C. solstitialis* abundance along the successional gradient (Figure 1). A threshold may suggest that at some abundance level of other organisms the plant community becomes increasingly resistant to the invasion of *C. solstitialis*. These perennial dominated communities would appear to be less susceptible to *C. solstitialis* invasion. A successional gradient threshold may imply that perennial grass effects are significant to reduce invasibility, and as such, allow some type of prediction to be made relative to weed management decisions.

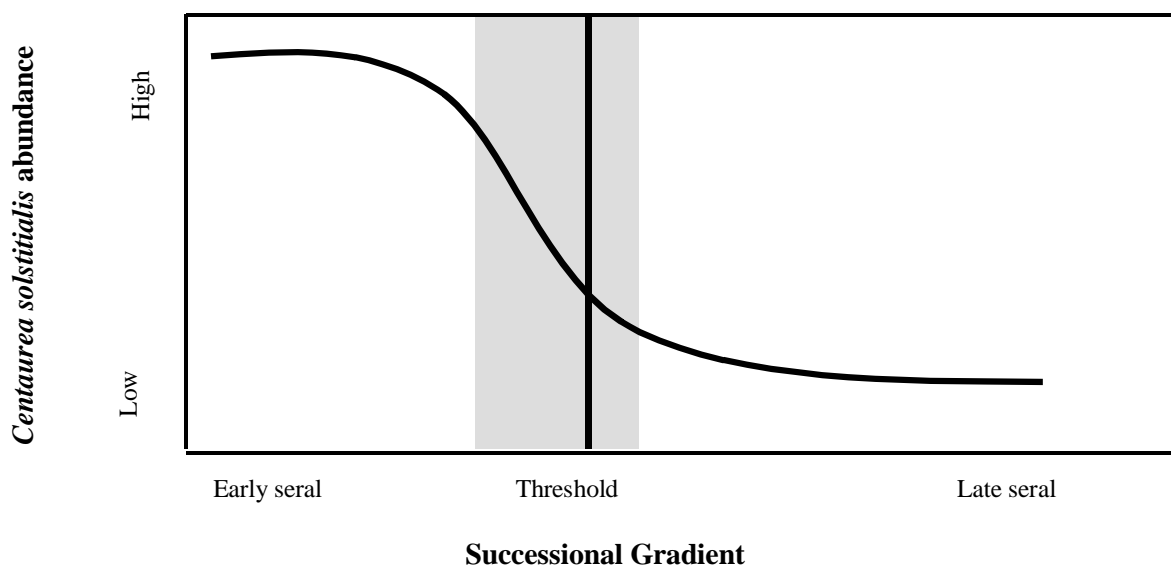


Figure 1. A Conceptual threshold along a successional gradient.

In addition, the intention of this research was to provide a foundation to identify a level of management sufficient to improve a habitat's condition in order to reduce its susceptibility to invasion by *C. solstitialis*. Management tools (i.e. replanting of desirable species, grazing management, biological weed control, herbicides, fire, etc.) may be necessary to manage *C. solstitialis* and other noxious weeds, thus accomplishing a shift of habitat characteristics beyond a threshold state to avoid or reduce further weed invasion.

LITERATURE REVIEW

Canyon grasslands

The canyon grasslands of the middle Snake River Canyon and its tributaries consist of a distinctive vegetation region of the Pacific Northwest (Tisdale 1986). The grasslands are a part of the Palouse Prairie, an intermountain bunchgrass vegetation type that originally extended throughout southwestern Canada, eastern Washington and Oregon, and southwestern Idaho and western Montana (Sims 1988).

Perennial bunchgrass communities dominate the canyon grasslands. The vast majority of canyon grassland communities are dominated by (You have previously called this Pseudoroeg?) *Agropyron spicatum* (bluebunch wheatgrass) and *Festuca idahoensis* (Idaho fescue) habitat types (Tisdale 1986). *Agropyron spicatum* has now been renamed *Pseudoroegneria spicata* [Pursh. A. Löve] (USDA, NRCS URL:<http://plants.usda.gov>) [Accessed 11 Oct. 2001]. The native grasslands of this region evolved with minimal grazing pressure. Rapid decline of the native perennial grasses has led to the widespread belief that these grasses were not adapted for grazing (Mack and Thompson 1982). The absence of grazing by *Bison bison*, likely has been an important factor in the decline of the bunchgrasses following grazing (Tisdale 1961).

Historical weed invasions

The canyon grasslands of the middle Snake River drainage historically have experienced a sequence of biological invasions by weeds. *Hypericum perforatum* was introduced to Oregon in the mid 1850's, and by 1945 had infested approximately 500,000 ha in Idaho (Tisdale 1976). During the 1950s and 1960s, *Hypericum perforatum* was

biologically controlled by insects, a great deal of the canyon land of northern Idaho was left with *Bromus tectorum* as a dominant plant species, and the habitats were subsequently invaded by *C. solstitialis* and other weeds. The removal of the *Hypericum perforatum* allowed the annual grasses to rapidly reestablish, preventing the return of the native perennial grass seedlings by competition. More recently *C. solstitialis* was introduced into the grasslands. *C. solstitialis* has been able to utilize more resources than the annual grasses and as a result *C. solstitialis* populations have expanded rapidly.

The grassland steppe of the Pacific Northwest and the California annual grasslands, once dominated by native perennial grasses such as *Pseudoroegneria spicata*, are examples of grasslands where perennial vegetation loss has been followed by *Bromus tectorum* domination (Sheley and Larson 1994). Invasive species have filled the gaps in the canyon grasslands caused by the loss of native perennials. Natural recovery of perennial plants is inhibited by inadequate seed source and competition from invasive plant species. Degraded rangeland dominated by invasive species is often devoid of competitive perennial plants. On these sites, rangeland weed control is often short-lived because desirable species are not available to occupy niches opened by weed control procedures (Sheley et al. 1996).

Hironaka (1990) proposed that the sequence of species replacement among winter annuals would be from early-maturing species to later-maturing ones (e.g. *Bromus tectorum* yields to *Taeniatherum caput-medusae* or *C. solstitialis*). In this scenario, *C. solstitialis* invades sites dominated by early-maturing invasive annual grasses through utilization of deep soil moisture to produce large numbers of propagules late in the season (Borman et al. 1991). Peters (1994) found islands of the perennial grass *Sitanion hystrix* might successfully resist *C. solstitialis*, promoting succession toward perennial dominance. Maturity date and

fecundity were cited as driving factors in a replacement series among annuals (Roché and Thill 2001). Introduced annual grass communities are susceptible to repeated disturbances and subsequent invasion by other species. The invasive plant communities persist because of constant recruitment into areas not closed by perennial vegetation (Wilson and McCaffrey 1999).

Cryptogams

Cryptogamic soil crusts are an important component of many arid rangeland ecosystems in the western United States. Such crusts have been found to reduce soil erosion and increase nitrogen fixation (Johansen and St. Clair 1986). Varying findings on the effect of cryptogamic crusts on perennial grass seedling establishment have been reported. Johansen and St. Clair (1986) found they enhanced seedling establishment while Schlatterer and Tisdale (1969) found moss litter inhibited seedling establishment. Development of cryptogamic crusts depends on the influences of soil characteristics, climate, competition from plant cover, and the effects of animal and human disturbance. Lichens and mosses are slow to recover from disturbance. Anderson et al. (1982) found that lichens and mosses, in a desert shrub community, had become fairly well established after a 14 to 17 year period of protection from grazing. An important aspect in the development of soil crusts is frequency and abundance of moisture. It is possible that in drier areas or drier years development of cryptogamic crusts following grazing disturbance might take longer (Johansen and St. Clair 1986).

Centaurea solstitialis

Centaurea solstitialis, a facultative winter annual of Mediterranean origin, is a serious rangeland invasive species in the western United States (Maddox et al. 1985). *C. solstitialis* infestations can reduce wildlife habitat and forage, displace native plants, and decrease native plant and animal diversity (Sheley and Larson 1994).

Introduction of *C. solstitialis* to the Pacific Northwest occurred in the mid 1800's (Talbot Roché and Thill 2001). During the 1920's, *C. solstitialis* was widely distributed as a contaminant in alfalfa seed and expanded rapidly in grasslands within the Pacific Northwest (Gerlach 1997). By the 1970's, *C. solstitialis* populations in many areas had joined together to occupy large, contiguous areas in Idaho, Oregon, and Washington. In the mid-1980's, *C. solstitialis* infestations were estimated to be about 113,000 ha in Idaho, 54,000 ha in Oregon, and 59,000 ha in Washington (Sheley et al 1999). The Idaho infestation had grown to 80,940 ha by 1989 (Callihan et al. 1989), and 202,350 ha by 1996 (Callihan and Lass 1996).

C. solstitialis's successful invasion of natural grasslands appear to be dominant on southeast to southwest facing slopes (Roché et al. 1994). South facing natural grasslands provide more favorable light and temperature conditions than do other habitats in the Pacific Northwest, and these grasslands are more susceptible to invasion by *C. solstitialis*. *C. solstitialis*'s success is fostered by rapid germination and seedling growth and by high production of small, easily dispersed and sometimes long-lived achenes that buffer against mortality among achenes and seedlings. These ruderal traits confer a greater adaptability for rapid spread and colonization of disturbance by *C. solstitialis* (Callihan 1993, Roché and Thill 2001).

The competitive success of *C. solstitialis* is directly related to its rapid growth and resource capture (Sheley et al. 1999), competition for moisture had more impact on establishing *Thinopyrum intermedium* (intermediate wheatgrass) than on *C. solstitialis* (Prather and Callihan 1991). *C. solstitialis* seedlings and rosettes require adequate light, water, nutrients, and space, and die easily under stressful conditions. With ample resources, *C. solstitialis* seedlings grow more rapidly than most perennial grass seedlings. This characteristic leads to poor grass stand establishment when grass seedlings are competing with *C. solstitialis*. Once established, however, stands of perennial grass can limit reinvasion by *C. solstitialis* (Larson and McInnis 1989).

Perennial grass competition

Centaurea solstitialis grows rapidly and continuously during the winter, giving it access to moisture stored deep in the soil profile not depleted by the native plants. Light intensity at the soil surface during the winter and residual soil moisture during the summer are two critical factors limiting its invasion (Roché et al. 1994).

In the *Pseudoroegneria spicata* community, the length of the growing season appears to be related to rooting zone soil moisture depletion (Roché et al. 1994). Native grassland species become dormant in summer, avoiding water stress during the summer. In contrast, *C. solstitialis* remains active, flowering and producing seed in July and August in these communities (Roché et al. 1994). *C. solstitialis* requires a different strategy to overcome the summer drought. In southwestern Oregon annual grasslands, *C. solstitialis* invaded by utilizing residual soil moisture left by earlier maturing annuals (Borman et al. 1992).

Perennial grass can limit *C. solstitialis* if it is managed to provide two conditions: 1) shade over the soil surface from fall through spring and 2) soil water depletion from late

spring through summer. Shallow soils do not have the potential to support enough vegetation to shade *C. solstitialis*, but in the absence of summer precipitation, perennials deplete soil moisture before *C. solstitialis* matures, thus limiting its competitiveness (Roché et al. 1994). Results of both field and controlled greenhouse studies suggest perennial grass dominated communities successfully compete with *C. solstitialis* (Prather 1989, 1990). Conversely, annual grass communities display high susceptibility to invasion by *C. solstitialis* (Prather 1989, Lindquist et al. 1996, Duke 2001.) *C. solstitialis* growth rates tend to decline as perennial plant density increases or soils become shallow (Sheley and Larson 1995). A shift in competitive ability under these conditions means that *C. solstitialis* will become a secondary or co-dominant species in the plant community (Sheley et al. 1999).

Borman et al. (1992) found that plants able to extract soil moisture and phenologically develop early in the year should have a competitive advantage over those that are active later in the year. The rosette of a winter annuals such as *C. solstitialis* provides it the advantage of increased photosynthetic capability, allowing both above and below ground growth during cold months. *C. solstitialis* exhibits rapid root extension during early winter, increasing taproot length by as much as tenfold between November and January (Roché et al. 1994). It then allocates resources to rapid rosette growth from January to April, in contrast to *Bromus tectorum*, which develops its adventitious root system during the cold months but lacks rosettes so has little above ground growth during that time.

Root partitioning between *C. solstitialis* and competing vegetation can influence its ability to invade grasslands. Sheley and Larson (1994) found the rooting depth of *C. solstitialis* is deeper than *Bromus tectorum* and suggest that differential rooting depth promotes the partition of resources. In this study, they speculate that *C. solstitialis* has the

potential in deep soils to grow faster and sequester more resources than most perennial grass seedlings. Germination and root dynamics of range weeds suggest that the later-maturing characteristic of *C. solstitialis* is benefited by rapid germination, radical elongation and root growth, and that these attributes increase the ability of *C. solstitialis* roots to penetrate to greater soil depths, extending the period of resource availability and the likelihood of increased seed production (Sheley et al. 1999).

Community invasibility

Plant ecologists have looked at invasibility from two related perspectives: 1) the plant community's characteristics that determine its susceptibility to invasion, and 2) the invasive plant's functional characteristics that make it a successful invasive species. Considerable work has been done to understand the properties of invasive species. More recently, plant ecologists have focused attention on the properties of communities that determine their invasibility.

While many studies suggest that diverse systems are more resistant to invasion than are less diverse systems (Elton 1958, Fox and Fox 1986, and Tilman 1997), a debate continues regarding the effects and importance of diversity relative to factors such as plant cover and disturbance. Elton (1958) suggested that greater community diversity results in greater invasion resistance. According to this concept, competition for the resources required by all plants is greater in diverse plant communities compared to communities with fewer species. The more intense competition for resources in species rich communities tends to prevent establishment of newly introduced species. In addition to competition with

established native species, losses caused by natural enemies and lack of mutualists and mates present possible barriers to invasion (Crawley 1987).

Results of a number of studies support the inverse correlation of diversity and invasibility (Tilman 1997, Symstad 2000, Dukes 2001), but others show both positive correlations (Planty-Tabacchi et al.1996, Wiser et al.1998, Smith and Knapp 1999, Levine 2000) and no relationship (Crawley et al.1999). These contradictory findings appear to reflect differing competitive interactions between species within resident functional groups (Dukes 2001). Functional groups include plants that are similar in the way they use and compete for resources ie. C₃ graminoids, forbs, and C₄ graminoids. Diversity effects may differ between microplot and larger community scales as well as between different resident functional groups (Dukes 2001).

Burke and Grime (1996) identified a closed cover of established species as the major factor reducing the probability of successful invasion. Crawley (1987) found the most invulnerable communities to have low levels of plant cover and be subject to frequent disturbance. A community is invulnerable when an introduced species is able to establish and persist or expand (Crawley 1987).

Abundant evidence points to disturbance as the critical predictive characteristic of plant community invasibility (Forcella and Harvey 1983, Crawley 1987, Tilman 1997, Hobbs and Huenneke 1992). Symstad (2000) found the response of resident functional groups to initial disturbance to be more important than the groups' richness and composition. Smith and Knapp (1999) found diversity of both native and invasive species positively related to the disturbance regime.

The disturbances that result in increases of invasive species are usually caused by human activities. Grasslands are particularly vulnerable to invasion when they are severely grazed. They have relatively frequent breaks in their natural plant cover where invaders can become established. The failure of invasion by introduced species can be related to the closed nature of the native vegetation competition.

The interactions of species diversity and composition with plant cover and disturbance have yet to be definitively defined. A principal characteristic of disturbance is freeing resources formerly captured by plants (Elton 1958). Communities are more susceptible to invasion at particular zones on an environmental gradient, and communities differ in their susceptibility along successional gradients (Forcella and Harvey 1983).

Ecological thresholds

Ecological thresholds are thought of as boundaries in space and time that separate one vegetation state from another (Friedel 1991). The concept of thresholds arose from models viewing changes in plant communities over time as series of transitions between states of vegetation progressing (or regressing) continuously along a successional continuum (Westoby et al. 1989, Laycock 1991, and Tausch et al. 1993). Friedel (1991) suggests that environmental change can be continuous with thresholds between alternative states. Two examples of thresholds are recognized in arid and semiarid rangelands: one separates grassland from woodland; and the other, stable from degraded soil. In both cases, crossing a threshold means the vegetation occupies a new domain and will not revert to its former state without intervention. Once a threshold is crossed to a more degraded state, the former state cannot be attained without significant management effort. Ecological thresholds may relate to

changes in community such as structure, nutrients and soil erosion due to factors such as competition and disturbance.

Attributes such as diversity, disturbance and plant cover are believed to be primary determinants of a plant community's invasibility. The competitive ability of perennial plants to influence the invasibility of canyon grassland communities by *C. solstitialis* has yet to be characterized. In this study, we ask the question does a threshold exist at which the presence of perennial plants along a successional gradient become a limiting factor to the invasion of *C. solstitialis*?

METHODS

Site Description

The area of the study is located at the Garden Creek Preserve on Craig Mountain in Idaho. Craig Mountain is located in southern Nez Perce and western Lewis counties, Idaho, about 16 km south of Lewiston (Figure 2). Craig Mountain is an east-sloping uplift that encompasses a plateau summit and associated steep canyon slopes between the Snake and lower Salmon rivers. The canyons are dominated by grasslands but include a mosaic of shrubland, riparian, coniferous forest and woodland habitats.

The Garden Creek Preserve, which is owned and cooperatively managed by the Bureau of Land Management (BLM), Cottonwood Resource Area, and The Nature Conservancy (TNC), was selected as the research area. The preserve is about 50 km south of Lewiston, Idaho and is approximately 5,670 ha in size. The study site is on moderately sloped benches that occur at mid canyon elevations from 762 to 1059 m. The preserve contains a variety of grassland habitat types (ht). Tisdale (1986) classified the vegetation of the grasslands into five habitat types consisting of *Carex hoodii/Festuca idahoensis* ht, *Festuca idahoensis/Koeleria cristata* ht, *Festuca idahoensis/Agropyron spicatum* ht, *Agropyron spicatum/Poa sandbergii/Balsamorhiza sagittata* ht, and *Agropyron spicatum/Opuntia polyacantha* ht. Tisdale uses *Poa sandbergii* in his habitat type description. *Poa sandbergii* taxonomy nomenclature has been changed to *Poa secunda* (USDA, NRCS URL: <http://plants.usda.gov> [Accessed 13 Apr. 2001]). The *Agropyron spicatum/Poa sandbergii/Balsamorhiza sagittata* ht is one of the most abundant habitat types in the study area and in the canyon grasslands. In this paper *Agropyron spicatum/Poa sandbergii*

Balsamorhiza sagittata ht will be indicated as *A. spicatum*/*P. sandbergii* ht. Although not presently grazed by domestic animals, the study area's grazing history has resulted in a complex of sites in varying successional stages from early to late seral. This habitat type is often severely impacted by *C. solstitialis*. *C. solstitialis* is most successful on annual grasslands with southeast to southwest facing slopes (Roché et al. 1994).

The study sites' soils are of the Kettenbach-Gwinn complex with 15 to 60% slopes. The Kettenbach series consist of moderately deep, well-drained soils and are classed as loamy-skeletal, mixed, superactive, mesic Pachic Argixerolls. The Gwin series consist of shallow, well-drained soils and are classed as loamy-skeletal, mixed, superactive, mesic Lithic Argixerolls (URL: <http://www.statlab.iastate.edu/soils/osd/> [Accessed 23 Mar 2001]). Both soils formed in colluvium and residuum from Columbia River basalt mixed with loess. Annual precipitation averages 35cm, most of which occurs from November through April.

Field methods and sampling procedures

Vegetation was sampled during the summers of 1999 and 2000 between May 26th and July 8th. Twenty five macroplots were located within two watersheds of the Garden Creek Preserve, Lower Corral Creek and China Garden Creek. The vegetation was classified into habitat types (Tisdale 1986). Homogeneous macroplots (25x25m) were selected representing different successional communities from within the *A. spicatum*/*P. sandbergii* ht. The sites were then field classified into successional stages (early, mid and late seral) in order to facilitate the distribution of macroplots along the successional gradient. The field classification corresponds approximately to the Natural Resource Conservation Service (NRCS) ecological condition classification system (Butler et al. 1997).

Criteria for macroplot selection included: 1) *A. spicatum*/*P. sandbergii* ht,

2) minimum plot size (25x25m), 3) aspect (southeast to southwest) and 4) accessibility.

Within each macroplot five randomly located 10m transects were established. Fifty microplots (20x50cm) were arranged systematically at one meter increments along the transects. Foliar cover of each vascular plant species was estimated using a cover class approach (Daubenmire 1959) as modified by the USDA Forest Service (1996). Seven cover classes were used corresponding to the following foliar cover intervals: 1 (0-1%), 2 (1-5%), 3 (5-25%), 4 (25-50%), 5 (50-75%), 6 (75-95%), 7 (95-100%). Percent canopy cover was determined by taking the midpoint value for each of the modified cover classes established for each microplot, summing these for all the microplots within that macroplot, and dividing by the number of microplots (50) per macroplot.

In addition, an ocular estimate of total plant, litter, cryptogams (lichens and mosses), bare ground and rock percent coverage was recorded for each microplot. Only lichens and mosses were estimated for cryptogamic cover and will be referred to as cryptogams hereafter. *C. solstitialis* density was obtained by counting individual plants in each microplot. Site characteristics recorded at each macroplot location included: 1) current vegetation, 2) habitat condition, 3) elevation, 4) aspect, 5) percent slope, and 6) soil type, color and texture. Location and elevation was recorded for each plot using a Garmin 12 global positioning system (GPS) (Appendix 1).

Statistical analyses

Cluster analysis of species composition was used to develop an initial classification of sites into successional stages (early, mid and late seral). Cluster analysis was conducted with percent canopy cover data using PC-ORD Statistical Ecology program (McCune and Mefford 1997).

Cluster analysis is a classification technique that groups the plots based on their overall resemblance to one another. Clustering algorithms are based on grouping similar stands based on overall variation between groups or among stands in comparison to another division or group. Similar plots will form clusters which are generally distinct from other clusters of plots. The agglomerative cluster model used begins with a collection of stands and progressively builds groups or cluster of similar stands. Clustering procedures operate on all possible pairwise combinations of distances between plots.

Relative Euclidean distance measure based on coverage was selected for the cluster analysis. Relative Euclidean Distance (RED) takes the average of coverage and develops composite composition for stands. This measure incorporates species abundance totals within each plot so that the final distance measure is relative to the differences in the total plots:

$$RED_{jk} = \sqrt{\sum_{i=1}^s \left[\left(\frac{X_{ij}}{\sum_i^s X_{ij}} \right) - \left(\frac{X_{ik}}{\sum_i^s X_{ik}} \right) \right]^2}$$

where RED is the Relative Euclidean Distance, X is foliar cover, i is ith species, jth and kth macroplot.

The Centroid Group mean clustering strategy (the unweighted pair-group method with arithmetic averages) was used to compute the mean of all distances between plots of one group to the plot of another. Once a group is formed, it is replaced by its mean and intercluster distances are those distances between these means or centroids. The results of cluster analysis are summarized in a hierarchical treelike structure called a dendrogram that shows relatedness of plots.

A univariate analysis was conducted on *C. solstitialis* and other variables to create an independent variable that would meet normality assumptions on the dependent variable.

Foliar cover data were grouped by life form: annual grasses, annual forbs, perennial grasses, and perennial forbs (See Appendix 2 for complete species list), which are independent variables used in the univariate analysis.

The relationships between cover estimate variables were summarized using nonparametric Spearman's Correlation Coefficients and their significance from zero tested. Correlations between *C. solstitialis*, perennial grass, cryptogams, litter, rock, bare ground, and slope were tested for significance ($P < 0.05$) using the correlation (CORR) procedure in SAS (1991).

In order to further examine the relationships between *C. solstitialis* and other variables, a linear regression model of the general form:

$$\ln(YS) = \beta_0 + \beta_1(PG) + \beta_2(CR) + e \quad (1)$$

where y (YS) is *C. solstitialis* abundance, expressed as percent foliar cover. β_0 is an intercept term, β_1 and β_2 are slope or rate terms related to percent foliar cover of perennial grasses (PG) and cryptogams (CR), respectively, was developed. E is an error term with usual linear regression assumptions.

The slope terms of this model are of interest because they provide quantitative measurement of size, degree and direction of any possible associations. All model fits were assessed using standard residual analysis. Statistical computations were carried out using SAS (1999).

Associations among *C. solstitialis* and other plant species within the community were analyzed at the microplot scale using plant species association with SPASSOC.BAS routine (Ludwig and Reynolds 1988). The species association analysis involves two components. The first is a statistical test of the hypothesis that two species are associated or not at a

predetermined probability level. The second is a measure of the degree of strength of the association. The procedure for species association is based on the presence or absence of species within microplots. The presence and absence is represented with binary data; presence is indicated with a 1 and absence with a 0.

RESULTS and DISCUSSION

Cluster analysis

The mean percent cover of each species for each macroplot (averaged for the two sampling seasons, 1999 and 2000) was included in the cluster analysis. The resulting cluster classification of seral stages corresponded well to the field determined classification. The results indicated a good representation in the data of the early, mid, and late seral stages (Table 1).

Table 1. Comparison between the seral stages in the field classification and the seral stages obtained by cluster analysis of cover estimate data.

Cluster Classification	Field Classification		
	Early seral	Mid seral	Late seral
Early seral	5	0	0
Mid seral	0	6	0
Late seral	0	2	8
Unclassified	1	3	0

The clustering of groups was stopped at a distance of 0.88 as a cut off point, resulting in three distinct groups at this level of resemblance. The pattern of clustering for the three groups is summarized in Figure 3. The late seral group is a cluster of 10 plots (3, 7, 16, 6, 13, 15, 20, 10, 12, and 25). The plots were joined at a clustering distance of 0.32. The shorter clustering distances between plots indicate greater degrees of similarity. The late seral group has the shortest clustering distance followed by the early, then mid, seral groups. The mid

seral group contains 6 plots (1, 19, 23, 21, 14, and 18) joined at a distance 0.80. The early seral group has five plots (2, 17, 5, 8, and 22), which are joined at a distance of 0.62. Four plots, 4, 9, 11, and 24, did not cluster into any of the three groups and are considered unclassified. Plots 9 and 11 have a high *Pseudoroegneria spicata* coverage combined with a high *C. solstitialis* coverage. Plot 11 has a high *C. solstitialis* coverage at 22.1%, and Plot 9 at 13.0%. *Pseudoroegneria spicata* has a coverage of 22.4% in Plot 11 and 24.2% for Plot 9. Plot 9 differs with its high *Bromus japonicus* (Japanese brome) cover (20.8%) compared to Plot 11 with 7.6% coverage. Both plots have *Vicia villosa* (winter vetch), an early seral species, present. Plots 24 and 4 both have a moderate cover of *Pseudoroegneria spicata* with low cover estimates of *C. solstitialis*. Plot 4 has a very high *Bromus tectorum* cover estimate at 10.3% compared to the rest of the plots, and *Balsamorhiza sagittata* is not present in this plot. Plot 24 has a high *Scutellaria angustifolia* (narrowleaf skullcap) cover estimate at 2.2%, and *Bromus tectorum* appears to have a low cover estimate at 1.6%.

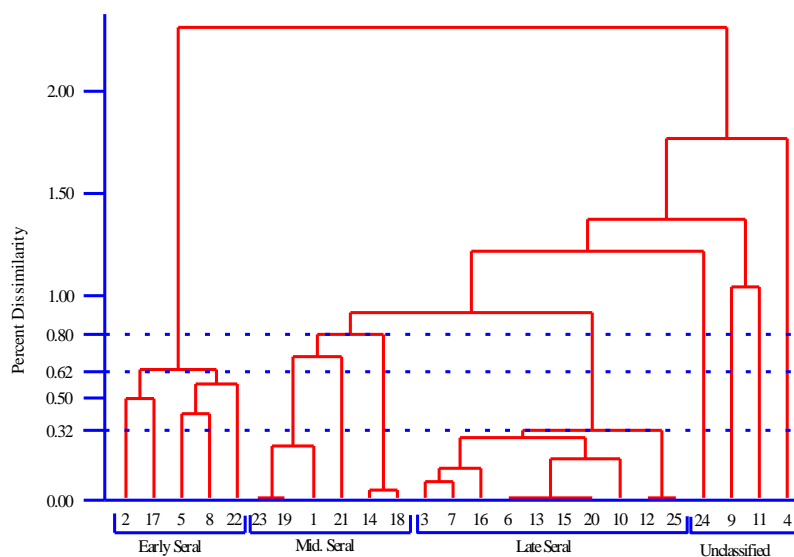


Figure 3. A dendrogram indicating the classification of successional stages by cluster analysis.

In order to further examine the species composition and abundances between the 3 groups, the mean percent cover of species greater than 1% in any macroplot for each group was analyzed. Of the 69 species only 17 species had greater than 1% cover in any macroplot. The species composition of these groups is summarized in Table 2. The species present were similar for the late and mid seral groups, but the perennial cover estimates differed among the 3 groups or seral stages. The late seral group had the highest coverage estimates of perennial species. *Pseudoroegneria spicata* was the dominant species with the highest cover, followed by *Balsamorhiza sagittata* (arrowleaf balsamroot), *Bromus japonicus*, *Lupinus sericeus* (silky lupine), *Achillea millefolium* (common yarrow) and *Astragalus arthurii* (waha milkvetch). The mid seral group had species present that were similar to the late seral group, except *C. solstitialis* is more prevalent and cover estimates are lower for the perennial species. The annual bromes, *Bromus japonicus* and *Bromus tectorum*, have the highest cover estimate in the mid seral group. The early seral group is characterized by the dominance of *C. solstitialis*, which has a mean cover of 32%. *Vicia villosa* is also common in this group and absent in the mid seral and late seral groups. *Balsamorhiza sagittata* has a higher cover estimate than *Pseudoroegneria spicata* in the early seral group.

Table 2. Mean percent cover and standard deviation of each species greater than 1% cover in any macroplot for early, mid, and late seral stages using Relative Euclidean Distance cluster analysis.

Species	Early seral		Mid seral		Late seral	
	<u>Mean</u>	<u>SD</u>	<u>Mean</u>	<u>SD</u>	<u>Mean</u>	<u>SD</u>
Annuals						
<i>Bromus japonicus</i>	5.67	2.69	11.66	3.12	4.15	2.17
<i>Bromus tectorum</i>	0.55	0.62	0.90	0.78	0.45	0.78
<i>Centaurea solstitialis</i>	31.51	6.03	2.19	3.23	0.57	0.95
<i>Festuca megalura</i>	0.61	0.91	0.00	0.00	0.00	0.00
<i>Vicia villosa</i>	1.95	3.45	0.00	0.00	0.00	0.01
Perennials						
<i>Achillea millefolium</i>	1.58	1.40	3.34	1.75	2.67	2.21
<i>Pseudoroegneria spicata</i>	5.94	1.28	17.09	2.18	25.20	3.86
<i>Astragalus arthuri</i>	0.16	0.21	0.60	0.94	0.34	0.40
<i>Astragalus cusickii</i>	0.04	0.08	0.90	0.99	0.69	1.26
<i>Balsamorhiza sagittata</i>	9.23	7.19	14.15	6.36	7.80	4.55
<i>Castilleja</i> spp.	0.05	0.11	0.33	0.41	0.02	0.07
<i>Lomatium triternatum</i>	0.20	0.21	0.37	0.28	0.45	0.81
<i>Lupinus sericeus</i>	3.85	2.35	3.96	0.38	2.79	1.34
<i>Opuntia polyacantha</i>	0.01	0.01	0.20	0.48	0.07	0.18
<i>Poa sandbergii</i>	0.12	0.15	0.16	0.14	0.31	0.39
<i>Scutellaria angustifolia</i>	0.82	1.05	0.31	0.65	0.93	1.18
<i>Zigadenus venenosus</i>	0.18	0.20	0.10	0.10	0.20	0.34

Correlation analysis

The strength of the associations at the macroplot scale between *C. solstitialis*, perennial grass cover, cryptogams (mosses and lichens), bare ground, rock, litter, and percent slope were quantified using Spearman's correlation coefficient. For example, 1999 *C. solstitialis* and perennial grass cover showed a correlation of -0.69 indicating that as one increased the other decreased. The prominent correlations are given in Table 3 (See Appendix 1, for all values).

Correlations were similar in magnitude and sign in both years. Results show that *C. solstitialis* is negatively correlated with perennial grasses, cryptogams, bare ground. Perennial grasses and cryptogams have a moderate positive correlation with each other. The negative correlation between perennial grass cover and *C. solstitialis* suggests possible competition for resources. Cryptogams are negatively correlated with slope and *C. solstitialis*.

Table 3. Spearman's correlations for selected vegetation and site variables for 2 sampling seasons (1999 and 2000).

	<i>Centaurea solstitialis</i>	Perennial grasses	Cryptogams	Slope
<u>1999 data</u>				
<i>Centaurea solstitialis</i>	1.00	-0.69*	-0.41*	-0.22
Perennial grass	-0.69*	1.00	0.40*	0.15
Cryptogams	-0.41*	0.40*	1.00	-0.62*
Slope	-0.22	0.16	-0.62*	1.00
<u>2000 data</u>				
<i>Centaurea solstitialis</i>	1.00	-0.76*	-0.54*	-0.14
Perennial grass	-0.76*	1.00	0.61*	-0.04
Cryptogams	-0.54*	0.61*	1.00	-0.58*
Slope	-0.14	-0.04	-0.58*	1.00

*Correlations followed by an asterisk are significant at P = 0.05.

Regression analysis

In most cases the abundance of *C. solstitialis* followed an exponential pattern of decrease with the increase of perennial grass cover and cryptogams. This nonlinear form can be linearized for estimation using a transformation, model (1), where the independent variables are perennial grasses and cryptogams.

Model estimations and residual analyses indicate an adequate fit with expected patterns and magnitudes for moderate slopes. Steep slopes indicated little relationship with perennial grasses and cryptogams. Parameter estimates are given in Table 4.

Initial examination of the data revealed segregation based on values for slope. Therefore, subsets of the macroplots representing steep (>43-60%) and moderate slope (15-43%) values were considered separately for the regression analysis.

The perennial grasses are more significant ($P = 0.0074$) in the steep slope regression model and not significant ($P = 0.1514$) in the moderate slope model (Table 4). The cryptogams are significant ($P = 0.0004$) in the moderate slope macroplots and not significant ($P = 0.6620$) in the steep slope macroplots for the 1999 data. The 2000 data were similar in comparison. The perennial grasses were more significant ($P = 0.0215$) in the steep slope model compared to ($P = 0.6030$) in the moderate slope model. The cryptogams were more significant in the moderate slope model ($P = 0.0204$) compared to ($P = 0.3313$) in the steep slope model. Cryptogams appear to have a significant negative relationship with steep slopes.

Table 4. Regression estimates of *Centaurea solstitialis* in relation to cryptogam and perennial grass cover, for 1999 and 2000 sampling seasons, at steep and moderate slope classes. Note: single space title and underline needed.

1999 data

<u>Slope</u>	<u>Parameter Estimate</u>	<u>SE</u>	<u>P> t </u>	<u>R²</u>
Steep >43-60%	$\beta_0 = 3.521$	0.988	0.0061	0.72
	$\beta_1 = -0.292$	0.648	0.6620	
	$\beta_2 = -0.192$	0.055	0.0074	
Moderate 15-≤43%	$\beta_0 = 4.981$	1.071	0.0009	0.81
	$\beta_1 = -0.245$	0.047	0.0004	
	$\beta_2 = -0.090$	0.058	0.1514	

2000 data

Steep >43-60%	$\beta_0 = 4.525$	0.963	0.0011	0.79
	$\beta_1 = -1.296$	1.100	0.3313	
	$\beta_2 = -0.219$	0.078	0.0215	
Moderate 15-≤43%	$\beta_0 = 3.447$	1.329	0.0268	0.66
	$\beta_1 = -0.184$	0.067	0.0204	
	$\beta_2 = -0.050$	0.094	0.6030	

Where β_0 = intercept of regression equation and β_1 (cryptogams) and β_2 (perennial grass cover) = slope of regression line and $P>|t| = 0.05$.

In general, the regression analyses indicated that perennial grasses and cryptogams have a negative relationship with *C. solstitialis* (Figures 4 and 5). The abundance of *C. solstitialis* cover decreases as perennial grasses increase in abundance. This may indicate that established perennial grasses and cryptogams have the ability to out compete *C. solstitialis*.

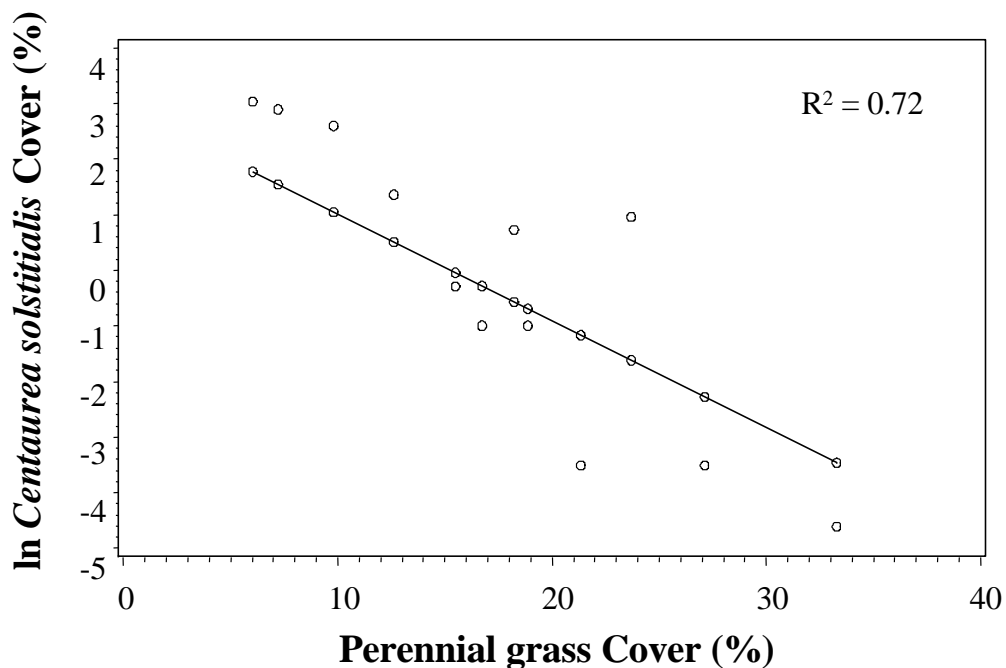


Figure 4. *Centaurea solstitialis* abundance in relation to perennial grass cover at slope of 43 - 60% using transformed data from the 1999 sampling season. $Y(\ln C. solstitialis) = x_1$ (cryptogams) - x_2 (perennial grass).

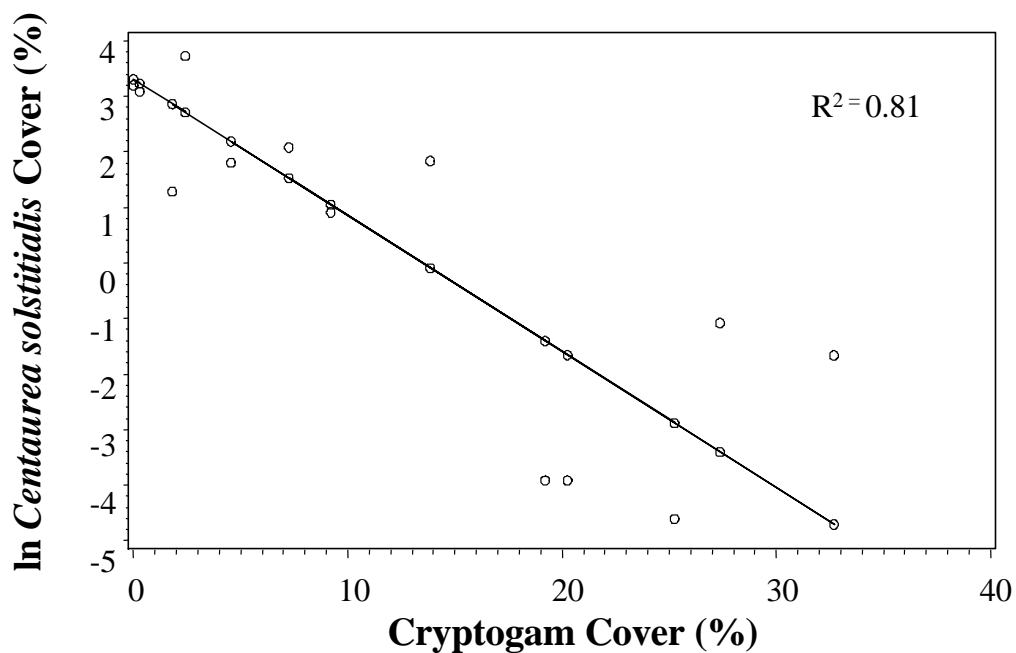


Figure 5. *Centaurea solstitialis* abundance in relation to cryptogam cover at slope of 15 - \leq 43% using transformed data from the 1999 sampling season. $Y(\ln C. solstitialis) = x_1$ (cryptogams) - x_2 (perennial grass).

Roché et al. (1994) suggests perennial grass can limit *C. solstitialis* if it is managed to provide two conditions: 1) shade over the soil surface from fall through spring and 2) soil water depletion from late spring through summer. Shallow soils do not have the potential to support enough vegetation to reduce *C. solstitialis* through shading, but in the absence of summer precipitation, perennials deplete soil moisture before *C. solstitialis* matures, limiting its competitiveness.

C. solstitialis also decreases as slope increases, perhaps due to harsher conditions. Environmental variables such as slope, aspect, and elevation have been used previously to determine the likelihood of occurrence for *C. solstitialis*. Lass et al. (1999) found that rangelands were predicted to have less *C. solstitialis* occurrence with increasing slope.

Cryptogams are shown to have a significant negative relationship with steep slopes, possibly due to site potential. On steep slopes succession may be slower due to a harsher site, shallower soils and/or lack of moisture. Moderate slopes may recover more quickly than steep slopes. Rate of succession is faster on moderate slopes due to deeper soils and more moisture (Belnap 1992). Succession may also affect the rate of recovery for cryptogams, though the cryptogam cover may be less for later successional stages on steep slopes. The recovery rate for lichens and mosses has been found to be extremely slow after severe disturbance (Belnap 1994).

Dunne (1989) reported that seeds easily germinate on bare soil, but rarely on cryptogamic crust. Seeds on the crust were prevented from coming into contact with mineral soil and, consequently, dried out and died. The successional pattern is altered when the crust is broken because it becomes a source of microsites for invasive grass establishment (Dunne 1989).

The cryptogams present a physical barrier that exclude establishment of *C. solstitialis* seedlings. Cryptogam cover may prevent *C. solstitialis* seeds from making contact with the soil, therefore not allowing the *C. solstitialis* seeds to germinate. However, cryptogams may also be a competitive factor in that the cryptogams directly use resources that otherwise seedlings of *C. solstitialis* would use.

The negative relationship of *C. solstitialis* abundance and cryptogam cover with steep slopes suggests that cryptogams and *C. solstitialis* may be more similar in response to slope as an environmental factor. On steep slopes cryptogam cover does not appear to affect the abundance of *C. solstitialis*, whereas on the moderate slopes the abundance of *C. solstitialis* increases as cryptogam cover decreases.

Plant association analysis

Associations among *C. solstitialis* and other plant species within the community were analyzed at the microplot scale. Species selected for the analyses had greater than 1% foliar cover throughout all macroplots. We assumed the species occurring at less than 1% cover did not have the potential to greatly affect *C. solstitialis* abundance or competition at the macroplot level. Five annual and 10 perennial species from the 1999 data, and five annual, 11 perennial species and cryptogams from the 2000 data were analyzed for plant association (Table 5). All annuals greater than 1% cover were non-native species except *Festuca megalura* (rat-tail fescue).

Species associations at the microplot scale reflected significant negative perennial species associations with *C. solstitialis*. The results indicate when there are high amounts of individual perennial species at the microplot level there are low amounts of *C. solstitialis*. However, individual perennial species at the microplot level that have significant negative

associations with *C. solstitialis* may not be able to exclude *C. solstitialis* occurrence at the macroplot scale because most of these species have a low percent cover at the macroplot scale. Probably only cryptogams, *Pseudoroegneria spicata*, and *Poa sandbergii* are adequately abundant to exclude *C. solstitialis* at the macroplot scale.

All annual species were positively associated with *C. solstitialis* except *Arenaria serpyllifolia* (thymeleaf sandwort), which was negatively associated with *C. solstitialis* in the 2000 data. Annual species tend to fluctuate more than perennial species from one year to the next. Changes in vegetation can be caused by climatic variation. Fluctuations in vegetation composition resulting from climatic variation may not necessarily produce a different plant community.

Table 5. Species associations among *C. solstitialis* and other plant species for 1999 and 2000 sampling seasons.

Species	1999		2000	
	Association	χ^2	Association	χ^2
Annuals				
* <i>Bromus japonicus</i>	+	1.831	+	16.158
* <i>Bromus tectorum</i>	+	5.105	+	7.502
<i>Festuca megalura</i>			+	79.520
* <i>Vicia villosa</i>	+	59.034	+	43.307
Perennials				
<i>Achillea millefolium</i>	-	20.868	-	0.672
<i>Pseudoroegneria spicata</i>	-	168.098	-	117.134
<i>Astragalus arthuri</i>	-	12.136	-	5.065
<i>Astragalus cusickii</i>	-	10.189	-	2.298
<i>Balsamorhiza sagittata</i>	-	0.139	-	1.167
<i>Castilleja</i> spp.	-	0.794	+	6.745
<i>Lomatium triternatum</i>	-	15.235	-	14.260
<i>Lupinus sericeus</i>	+	0.088	+	1.545
<i>Opuntia polyacantha</i>	-	0.212	-	2.458
<i>Poa sandbergii</i>	-	18.343	-	18.998
<i>Scutellaria angustifolia</i>	+	0.885	+	10.580
<i>Zigadenus venenosus</i>			+	0.003
Cryptogams				
Mosses and lichens (<i>Cladonia</i> spp. <i>Peltigera</i> sp. <i>Tortula ruralis</i>)	-	76.827	-	116.587

Bold indicates Chi-Square value significant at (P.05>3.8415)

OCHIAI Chi-Square value (corrected)

*non-native species

Successional gradient threshold

Examination of the non-transformed data shows relationships between *C. solstitialis* abundance and changes in community composition. As perennial grass and cryptogam cover increases in the community, *C. solstitialis* cover decreases. When perennial grass and cryptogam coverage exceeds 10%, the density of *C. solstitialis* is reduced (Figure 6).

The non-transformed data also reveal a division between steep and moderate slopes. Results show a relationship between cryptogam cover and the division of the two slope classes (Figure 7). Slope appears to be a factor affecting the abundance of cryptogams and *C. solstitialis*, both of which are lower on steep slopes than on moderate slopes. On moderate slopes, the abundance of both perennial grasses and cryptogams increase as *C. solstitialis* abundance decreases.

If a linear relationship between perennial grasses/cryptogams and *C. solstitialis* existed, there would be continuously decreasing amounts of perennial grasses and cryptogams associated with continuously increasing amounts of *C. solstitialis*. A linear relationship would indicate no threshold exists.

In contrast this study's data shows a curvilinear relationship between perennial grass/cryptogam and *C. solstitialis* abundance. As perennial grasses and cryptogams increase at the same rate, *C. solstitialis* decreases at a changing rate. When total coverage of perennial grass and cryptogam is less than 10% and 6%, *C. solstitialis* cover increases at an accelerated rate. The system appears to behave differently on either side of the transitional zone. For example, when perennial grass and cryptogam cover increases above 10% and 6%

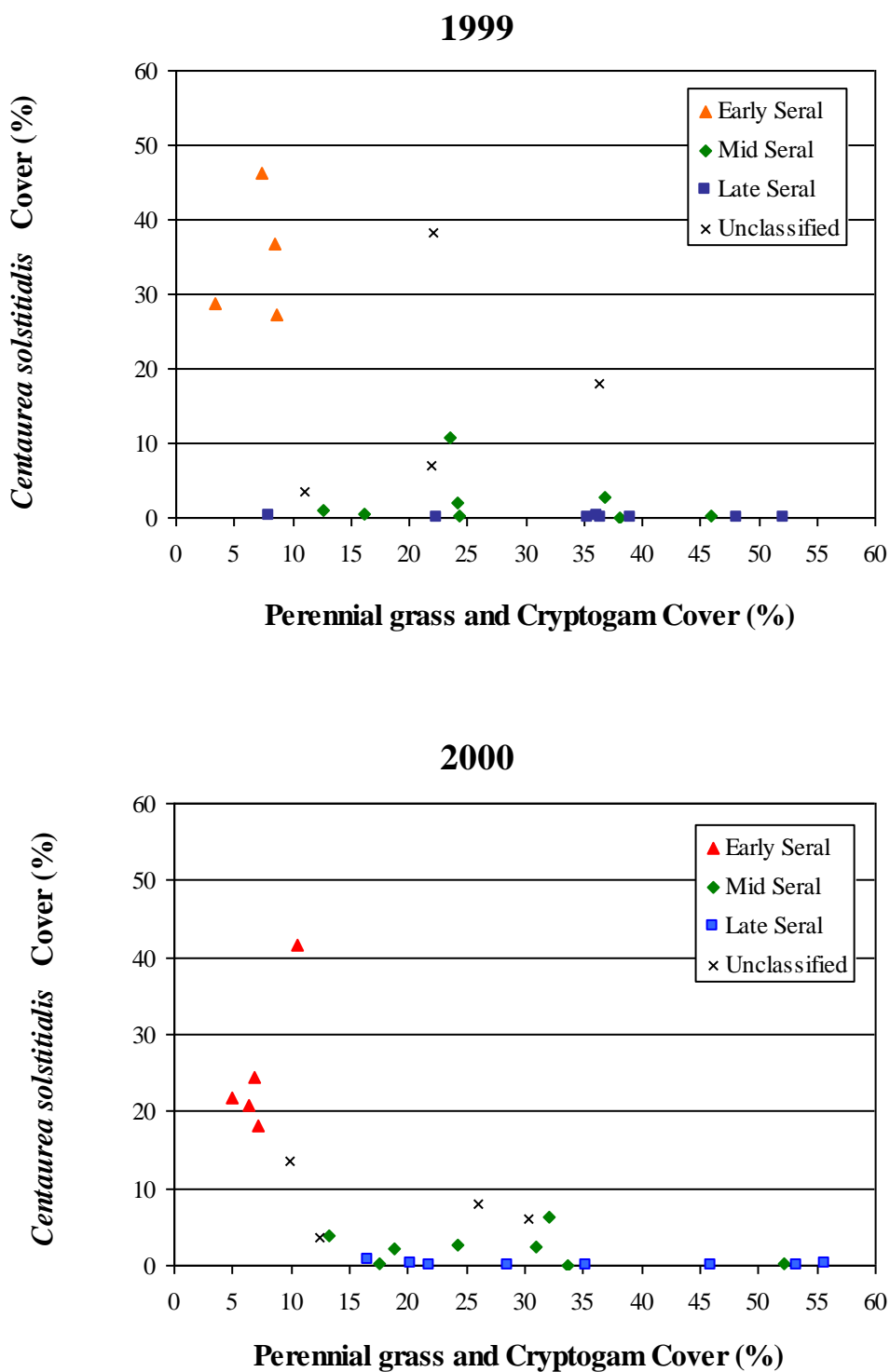


Figure 6. *Centaurea solstitialis* abundance in relation to perennial grass and cryptogam cover by successional stage using non-transformed data from the 1999 and 2000 sampling seasons.

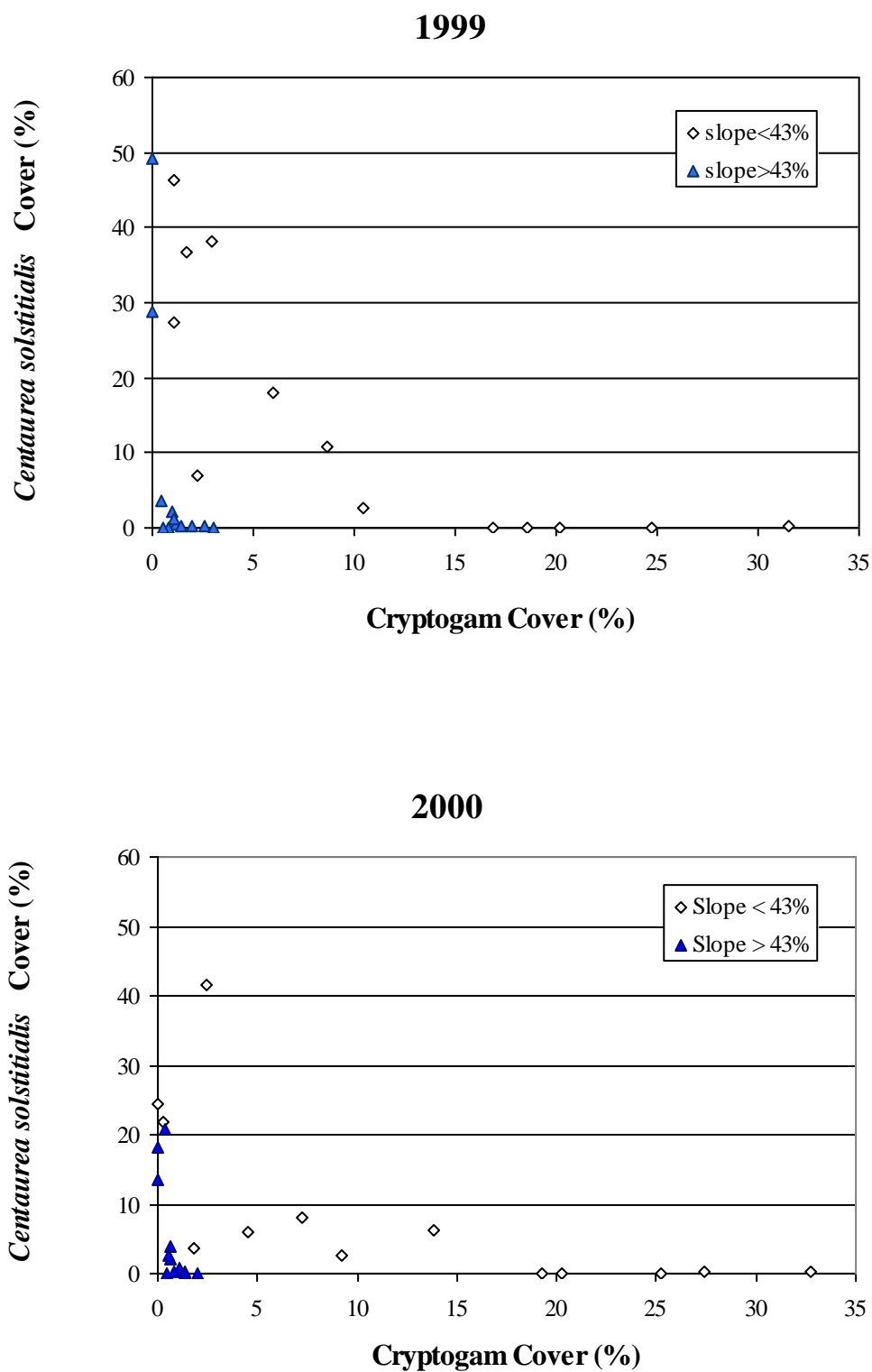


Figure 7. *Centaurea solstitialis* abundance in relation to cryptogam cover by slope class using non-transformed data from the 1999 and 2000 sampling seasons.

respectively, *C. solstitialis* cover is relatively constant. The transition zone may also change with climatic variation and herbivore use.

This curvilinear relationship suggests a threshold may exist at which *C. solstitialis* can no longer invade communities dominated by perennial plants. The position of the threshold clearly reflects the contrast in composition between annual dominated early seral and perennial dominated mid and late seral grassland communities.

Competition from perennial grasses and a barrier to germination from cryptogams appear to limit *C. solstitialis* invasion. Competition is inferred by species composition based on foliar cover estimates. The existence of a threshold would suggest that at some abundance level of perennial grasses and/or cryptogams the plant community is resistant to the invasion of *C. solstitialis*.

CONCLUSION

A threshold of perennial grasses and cryptogam cover appears to exist, above which the integrity of canyon grassland communities is maintained and below which these communities are susceptible to invasion by *C. solstitialis*.

The percent total coverage of perennial grasses and cryptogams along the successional gradient shows a curvilinear relationship with *C. solstitialis*, which suggests a threshold exists at 10 to 15% cover. If, instead, a linear relationship between perennial grasses/cryptogams and *C. solstitialis* had been shown, there would have been continuously decreasing amounts of perennial grasses and cryptogams associated with continuously increasing amounts of *C. solstitialis* congruent with the successional gradient. Such a linear relationship would have indicated no threshold exists.

Slope was a significant factor in regression analysis. *C. solstitialis* and cryptogams had a negative relationship with steep slopes, which may be due to site potential; cryptogamic cover decreases as slope increases. On steep slopes succession may be slower due to a harsher site, shallower soils and/or lack of moisture. The negative relationship of *C. solstitialis* abundance and cryptogam cover with steep slopes suggests that cryptogams and *C. solstitialis* may be more similar in response to slope as an environmental factor. Competitive interactions with perennial grasses appear more important for reducing *C. solstitialis* on steep slopes than on moderate slopes.

The relationships at the macroplot scale between *C. solstitialis* and perennial grass and cryptogamic cover shows a negative correlation, indicating that as one increased the

other decreased. The negative correlation between perennial grass cover and *C. solstitialis* also suggests probable competition for resources.

The presence of a threshold aid in formulation of attainable weed management goals for canyon grasslands may be identified. Abundance levels of perennial grass and cryptogamic cover may predict invasibility by *C. solstitialis*. Furthermore, established perennial grass cover as low as 10 to 15% may be sufficient to resist invasion. Management objectives could focus on increasing perennial grass cover to at least 10% to make a site less susceptible to invasion. On moderate slopes, reducing disturbance should enhance development of cryptogams, further enhancing the site's resistance to invasion by yellow starthistle.

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Appendix 1. UTM and Latitude/Longitude coordinates for the study plots at Garden Creek Preserve, Idaho.

Study plots	Easting	Northing	Latitude	Longitude
	506883	5099863	116.911025120	46.054268827
	506884	5099862	116.911012207	46.054259817
	509059	5099204	116.882909079	46.048312272
	508451	5098484	116.890780459	46.041839829
	508086	5098338	116.895500137	46.040530193
	508134	5098242	116.894881446	46.039665594
	508143	5098219	116.894765529	46.039458479
	507750	5098391	116.899841583	46.041011098
	507776	5098346	116.899506302	46.040605789
	507793	5098364	116.899286308	46.040767601
	509879	5095853	116.872379739	46.018140838
	509806	5095781	116.873324255	46.017493863
	507234	5099539	116.906492755	46.051349107
	507255	5099531	116.906221429	46.051276882
	507222	5099491	116.906648595	46.050917219
	509828	5095744	116.873040817	46.017160534
	509838	5095716	116.872912214	46.016908381
	509596	5095593	116.876040848	46.015804771
	509188	5095771	116.881307869	46.017412429
	509517	5095555	116.877062110	46.015463860
	509427	5095803	116.878219802	46.017697192
	509378	5095768	116.878853482	46.017382852
	508987	5095565	116.883908295	46.015561023
	508990	5095552	116.883869787	46.015443979
	508474	5098465	116.890483549	46.041668539

Appendix 2. Species list for plants occurring on the study area at Garden Creek Preserve, Idaho. Taxonomy follows USDA, NRCS. 2001. The PLANTS Database, Version 3.1 (<http://plants.usda.gov>). National Plant Data Center, Baton Rouge, LA 70874-4490 USA.

Symbol	Scientific name	Common name
ACMI2	<i>Achillea millefolium</i> L.	common yarrow
AGOSE	<i>Agoseris</i> sp. Raf.	agosaris
ALAL3	<i>Alyssum alyssoides</i> (L.) L.	pale madwort
AMRE2	<i>Amsinckia menziesii</i> var. <i>menziesii</i> (Lehm.) A. Nels. & J.F. Macbr.= <i>Amsinckia retrorsa</i> Suksdorf	Menzies' fiddleneck
ARSE2	<i>Arenaria serpyllifolia</i> L.	thymeleaf sandwort
ARLU	<i>Artemisia ludoviciana</i> Nutt.	white sagebrush
ASAR8	<i>Astragalus arthurii</i> M.E. Jones	waha milkvetch
ASCU5	<i>Astragalus cusickii</i> Gray	Cusick's milkvetch
ASIN5	<i>Astragalus inflexus</i> Dougl. ex Hook.	bent milkvetch
BASA3	<i>Balsamorhiza sagittata</i> (Pursh) Nutt.	arrowleaf balsamroot
BLSC	<i>Blepharipappus scaber</i> Hook.	rough eyelashweed
BRASS2	<i>Brassica</i> L.	mustard
BRBR5	<i>Bromus briziformis</i> Fisch. & C.A. Mey. = <i>Bromus brizaeformis</i> Fischer & C. Meyer	rattlesnake brome
BRJA	<i>Bromus japonicus</i> Thunb. ex Murr.	Japanese brome
BRTE	<i>Bromus tectorum</i> L.	cheatgrass
CAMAM	<i>Calochortus macrocarpus</i> Dougl. var. <i>maculosus</i> (A. Nels. & J.F. Macbr.) A. Nels. & J.F. Macbr.	Nez Perce mariposa lily
CAHI9	<i>Castilleja hispida</i> Benth.	harsh Indian paintbrush
CESO3	<i>Centaurea solstitialis</i> L.	yellow star-thistle
CIUN	<i>Cirsium undulatum</i> (Nutt.) Spreng.	wavyleaf thistle
CLPU	<i>Clarkia pulchella</i> Pursh	pinkfairies
COGR4	<i>Collomia grandiflora</i> Dougl. ex Lindl.	grand collomia
CREPI	<i>Crepis</i> L.	hawksbeard
CRIN8	<i>Cryptantha intermedia</i> (Gray) Greene	Clearwater cryptantha
DRVE2	<i>Draba verna</i> L.	spring draba
EPBR3	<i>Epilobium brachycarpum</i> K. Presl= <i>Epilobium paniculatum</i> Nutt. ex Torr. & Gray	tall annual willowherb
ERNAS2	<i>Ericameria nauseosa</i> (Pallas ex Pursh) Nesom & Baird ssp. <i>nauseosa</i> var. <i>speciosa</i> (Nutt.) Nesom & Baird= <i>Chrysothamnus nauseosus</i> (Pallas ex Pursh) Britt.	rubber rabbitbrush
ERPU2	<i>Erigeron pumilus</i> Nutt.	shaggy fleabane
ERC16	<i>Erodium cicutarium</i> (L.) L'Hér. ex Ait.	redstem stork's bill
ERCAC	<i>Erysimum capitatum</i> (Dougl. ex Hook.) Greene var. <i>capitatum</i> = <i>Erysimum asperum</i> (Nutt.) DC.	sanddune wallflower

GAAP2	<i>Galium aparine</i> L.	stickywilly
HYPE	<i>Hypericum perforatum</i> L.	common St. Johnswort
LASE	<i>Lactuca serriola</i> L.	prickly lettuce
LARA	<i>Lagophylla ramosissima</i> Nutt.	branched lagophylla
LIPA5	<i>Lithophragma parviflorum</i> (Hook.) Nutt. ex Torr. & Gray	smallflower woodland-star
LIRU4	<i>Lithospermum ruderales</i> Dougl. ex Lehm.	western stoneseed
LOAR5	<i>Logfia arvensis</i> (L.) Holub = <i>Filago arvensis</i> L.	field cottonrose
LODI	<i>Lomatium dissectum</i> (Nutt.) Mathias & Constance	fernleaf biscuitroot
LOTR2	<i>Lomatium triternatum</i> (Pursh) Coult. & Rose	nineleaf biscuitroot
LUSE4	<i>Lupinus sericeus</i> Pursh	silky lupine
MAGR3	<i>Madia gracilis</i> (Sm.) Keck & J. Clausen ex Applegate	grassy tarweed
MYST2	<i>Myosotis stricta</i> Link ex Roemer & J.A. Schultes = <i>Myosotis micrantha</i> auct. non Pallas ex Lehm.	strict forget-me-not
OPPO	<i>Opuntia polyacantha</i> Haw.	plains pricklypear
PHHE2	<i>Phacelia heterophylla</i> Pursh	varileaf phacelia
PHLI	<i>Phacelia linearis</i> (Pursh) Holz.	threadleaf phacelia
PHCO10	<i>Phlox colubrina</i> Wherry & Constance	Snake River phlox
PLPA2	<i>Plantago patagonica</i> Jacq.	woolly plantain
POBU	<i>Poa bulbosa</i> L.	bulbous bluegrass
POSA12	<i>Poa pratensis</i> L.	Kentucky bluegrass
POSE	<i>Poa secunda</i> J. Presl = <i>Poa sandbergii</i> Vasey	Sandberg bluegrass
PODO4	<i>Polygonum douglasii</i> Greene	Douglas' knotweed
POGR9	<i>Potentilla gracilis</i> Dougl. ex Hook	slender cinquefoil
PSSP6	<i>Pseudoroegneria spicata</i> (Pursh) A. Löve = <i>Agropyron spicatum</i> (Pursh) Scribn. & J.G. Sm.	bluebunch wheatgrass
SCAN3	<i>Scutellaria angustifolia</i> Pursh	narrowleaf skullcap
SENEC	<i>Senecio</i> L.	ragwort
SIAN2	<i>Silene antirrhina</i> L.	sleepy silene
SIAL2	<i>Sisymbrium altissimum</i> L.	tall tumbled mustard
SOMI2	<i>Solidago missouriensis</i> Nutt.	Missouri goldenrod
STNI	<i>Stellaria nitens</i> Nutt.	shiny chickweed
TONEL	<i>Tonella</i> Nutt. ex Gray	tonella
TRDU	<i>Tragopogon dubius</i> Scop.	yellow salsify
VALO	<i>Valerianella locusta</i> (L.) Lat.	Lewiston cornsalad
VEBL	<i>Verbascum blattaria</i> L.	moth mullein
VEAR	<i>Veronica arvensis</i> L.	corn speedwell
VIVI	<i>Vicia villosa</i> Roth	winter vetch
VUMY	<i>Vulpia myuros</i> (L.) K.C. Gmel. = <i>Festuca megalura</i> Nutt	rat-tail fescue
ZIVE	<i>Zigadenus venenosus</i> S. Wats.	meadow deathcamas

Appendix 3. Correlation coefficients matrix of biological and environmental variables based on cover value of the *Agropyron spicatum* –*Poa sandbergii*/*Balsamorhiza sagittata* habitat type. Correlations are significant at P = 0.05. N = 25.

1999	<i>Centaurea solstitialis</i>	Perennial Grasses	Perennial Forbs	Annual Grasses	Annual Forbs	Cryptogams	Slope	Litter	Rock	Bareground
<i>Centaurea solstitialis</i>	1.00	-0.694 0.0001	-0.188 0.3669	0.167 0.4224	0.493 0.0122	-0.410 0.0415	-0.221 0.286	0.764 <.0001	-.337 0.0992	-0.486 0.0137
Perennial Grasses	-0.069 0.0001	1.00	0.057 0.7841	-0.055 0.7940	-0.452 0.0232	0.407 0.0431	0.157	-0.505 0.0100	0.176 0.3996	0.492 0.0124
Perennial Forbs	-0.188 0.3669	0.057 0.4841	1.00	0.111 0.5968	-0.002 0.9913	-0.109 0.6032	0.310 0.1305	-0.041 0.843	0.263 0.2039	0.132 0.528
Annual Grasses	0.167 0.4224	-0.055 0.7940	0.111 0.5968	1.00	0.074 0.7229	0.175 0.4006	-0.071 0.7336	0.241 0.2447	0.113 0.5891	-0.279 0.175
Annual Forbs	0.493 0.0122	-0.452 0.0232	-0.002 0.9913	0.074 0.7229	1.00	-0.451 0.0235	0.053 0.7994	0.297 0.1484	-0.190 0.3610	-0.271 0.1892
Cryptogams	-0.410 0.0415	0.407 0.0431	-0.109 0.6032	0.175 0.4006	-0.451 0.1235	1.00	-0.623 0.0009	-0.334 0.1021	-0.206 0.3210	0.040 0.8466
Slope	-0.221 0.2863	0.157 0.4521	0.310 0.1305	-0.071 0.7336	0.053 0.7994	-0.623 0.009	1.00	-0.204 0.3259	0.522 0.0074	0.357 0.0794
Litter	0.764 <.0001	-0.505 0.0100	-0.041 0.8437	0.241 0.2447	0.297 0.1484	-0.334 0.1021	-0.204 0.3259	1.00	-0.410 0.0414	-0.713 <.0001
Rock	-0.337 0.092	0.176 0.3996	0.263 0.2039	0.113 0.5891	-0.190 0.3610	-0.206 0.3210	0.522 0.0074	-0.410 0.0414	1.00	0.199 0.3397
Bareground	-0.486 0.0137	0.492 0.0124	0.132 0.5284	-0.279 0.1758	-0.271 0.1892	0.040 0.8466	0.357 0.0794	-0.713 <.0001	0.199 0.3397	1.00

Appendix 3. Continued. Correlation coefficients matrix of biological and environmental variables based on cover value of the *Agropyron spicatum* – *Poa sandbergii*/*Balsamorhiza sagittata* habitat type. Correlations are significant at P = 0.05. N = 25.

2000	<i>Centaurea solstitialis</i>	Perennial Grasses	Perennial Forbs	Annual grasses	Annual Forbs	Cryptogams	Slope	Litter	Rock	Bareground
Centaurea Solstitialis	1.000	-0.761 <.0001	-0.086 0.6793	0.433 0.0304	0.280 0.1749	-0.542 0.0051	-0.142 0.4971	0.221 0.2868	-0.163 0.4357	-0.496 0.0116
Perennial Grasses	-0.761 <.0001	1.000	0.163 0.4361	-0.317 0.121	-0.259 0.210	0.616 0.001	-0.040 0.847	-0.053 0.8011	0.163 0.4361	0.348 0.0874
Perennial Forbs	-0.086 0.6793	0.163 0.4361	1.000	-0.243 0.2401	-0.542 0.0051	0.141 0.4997	-0.015 0.9432	-0.136 0.5140	-0.228 0.2720	-0.331 0.1058
Annual Grasses	0.433 0.0304	-0.317 0.1217	-0.243 0.2401	1.00	0.293 0.1540	-0.365 0.0727	0.500 0.8121	-0.007 0.9971	-0.088 0.6741	-0.505 0.0100
Annual Forbs	0.280 0.1749	-0.259 0.2108	-0.542 0.0051	0.293 0.1540	1.000	-0.351 0.0844	0.097 0.6418	-0.203 0.3303	0.233 0.2606	0.0126 0.9520
Cryptogams	-0.542 0.0051	0.616 0.0010	0.141 0.4997	-0.365 0.0727	-0.351 0.0844	1.000	-0.580 0.0023	-0.135 0.5199	-0.219 0.2914	0.144 0.4902
Slope	-0.142 0.4971	-0.040 0.8478	-0.015 0.9432	0.050 0.8121	0.097 0.6418	-0.580 0.0023	1.000	-0.102 0.6247	0.441 0.0270	0.192 0.3553
Litter	0.221 0.2868	-0.053 0.8011	-0.136 0.5140	-0.000 0.9971	-0.203 0.3303	-0.135 0.5199	-0.102 0.6247	1.00	0.114 0.5854	0.078 0.709
Rock	-0.163 0.4357	-0.086 0.6795	-0.228 0.2720	-0.088 0.6741	0.233 0.2606	-0.219 0.2914	0.441 0.027	0.114 0.5854	1.00	0.255 0.2171
Bareground	-0.496 0.0116	0.348 0.0874	-0.3312 0.1058	-0.505 0.0100	0.126 0.9520	0.144 0.4920	0.192 0.3553	0.078 0.7092	0.255 0.2471	1.00

