AN ABSTRACT OF THE THESIS OF

Kara Hempy Mayer for the degree of Master of Science in Botany and Plant Pathology presented on July 15, 2004.

Title: The Effects of Defoliation on *Bromus tectorum* Seed Production and Growth.

Abstract approved:

Redacted for privacy

David A. Pyke and Mark V. Wilson

Cheatgrass (*Bromus tectorum* L.) is a widespread exotic weed in the Intermountain sagebrush steppe. An annual grass, it is highly prolific and very competitive with native perennial grass seedlings. A clipping experiment carried out at two cheatgrass-dominated sites (Lincoln Bench and Succor Creek) in eastern Oregon analyzed effects of defoliation on cheatgrass seed production, investigated mechanisms of altered seed production and plant recovery, and considered the potential of defoliation as a cheatgrass control method. Treatments involved hand clipping plants at two heights (tall – 7.6-cm (T) and short – 2.5 cm (S)), two stages of phenological development (boot (B) and purple (P) stages), and two frequencies (once (1) and twice (2)), though purple stage clippings were clipped only once. Treatments were replicated in a randomized complete block design, which included a control with no defoliation. End of season seed production (seeds/m^2), plant density (plants/m^2), plant seed production (seeds/plant), and tiller production (percentage of plants with greater than 1 inflorescence) were estimated by sampling plants and litter from each treatment plot at the end of the growing season. Seeds were hand-collected from these samples, counted, and tested for viability. Soil moisture was measured with a TDR device in three randomly selected blocks, and averaged over the season for each treatment. End of season seed production was greater than zero for all treatments at both sites. At Lincoln Bench, all treatments excluding the TB1 treatment produced significantly less seed than the control. At Succor Creek, only the SB2 and SP treatments produced significantly less seed than the control. The SB2 treatment had the lowest seed

production at both sites, at 119 and 1243 seeds/m^2 at Lincoln Bench and Succor Creek, respectively, along with the SP treatment at 1115 seeds/m^2 at Succor Creek. The response patterns for plant density and seed production of individual plants were similar to that for overall seed production, which suggests that these treatments reduced seed production by increasing plant mortality and reducing plant reproductive ability. Tiller production increased for the SB1 treatment, which suggests that cheatgrass plants were able to recover from defoliation partly through asynchronous or increased tiller development. There was no significant effect of treatment on seasonal soil moisture. In conclusion, although the SB2 and SP treatments showed the greatest reduction in seed production, plants in these treatments still produced viable seed. Thus, applying a similar defoliation treatment for seedbed preparation with livestock—assuming similar treatment effects— may not be sufficient by itself to reduce cheatgrass to levels low enough to reduce competition in native reseeding projects. Alternatively, defoliation treatments could be intensified, and/or combined with other weed control methods as part of an integrated weed management approach.

The Effects of Defoliation on *Bromus tectorum* Seed Production and Growth

by

Kara Hempy Mayer

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DEDICATION

To my Michael and my Ella.

The Effects of Defoliation on *Bromus tectorum* Seed Production and Growth

Introduction

Aggressive non-native plants have been rapidly spreading into disturbed rangelands of the western Intermountain sagebrush steppe ecosystem of the United States since their introduction by European settlement in the late 1800's (Mack 1986). Of these, cheatgrass (*Bromus tectorum* L.) — a winter annual grass from Eurasia — is one of the most widespread, having infested approximately 7 million ha of public land or 18% of the land area in a five-state area within the region (Pellant and Hall 1994). In much of this area cheatgrass has become or is becoming the dominant plant, creating nearly homogenous annual grasslands in place of the perennial-dominated sagebrush steppe (Pellant and Hall 1994). This altered landscape diminishes both human resources and the stability of the sagebrush steppe ecosystem (DiTomaso 2000). Although cheatgrass is palatable to wildlife and livestock before seed maturation, its annual productivity is more variable than that of native bunchgrasses and remains palatable for a shorter period of time (Klemmedson and Smith 1964; West 1983; Mosley 1996). Forage production is consequently less predictable and consistent from year to year. Cheatgrass litter also creates an abundance of fine fuel that has led to a decrease in natural fire intervals, facilitating the further spread of cheatgrass (Young and Evans 1978; West 1983; Billings 1990; Whisenant 1990). This drastic shift in community composition may be altering ecosystem processes such as nutrient cycling (Evans et al. 2001), changing or reducing habitat and forage for wildlife, decreasing floral diversity, and facilitating the influx of secondary, non-palatable weeds such as yellow starthistle (*Centaura solstitialis* L.) (West 1983; Billings 1990; Northam and Callihan 1994; Sheley and Larson 1994).

To improve ecosystem conditions, attempts are being made to reestablish native grasses, shrubs, and forbs into disturbed sites through artificial seeding and transplanting techniques (Pellant 1990; Sanders 1994; Novak et al. 2001). However, establishing native seedlings in the presence of cheatgrass is a major obstacle. Cheatgrass preempts soil moisture through early and rapid germination and root development, thereby reducing soil moisture availability to later-developing native perennial seedlings (Harris 1967; Harris and Wilson 1970; Harris 1977; Aguirre and Johnson 1991; Nasri and Doescher 1995; Francis and Pyke 1996; Goodwin et al. 1996). It is also highly prolific, and once present in a disturbed area can spread quickly, further depleting resources available to native seedlings and young plants (Young and Evans 1985; Young et al. 1987). Consequently, the presence of cheatgrass in a restoration area can reduce native seedling survival and has been identified as one of the major causes for seedling failure in restoration projects (Whisenant 1999). To improve restoration success, the cheatgrass population must be eliminated or at least severely reduced before planting native species (Hull and Pearse 1943; Stark et al. 1946; Klemmedson and Smith 1964; Sanders 1994).

The use of directed intensive livestock grazing has been proposed as a potential cheatgrass control method (Vallentine and Stevens 1994; Miller et al. 1994; Mosley 1996; Novak et al. 2001). In light of the expense and uncertain effectiveness of other cheatgrass control methods such as herbicide application, mechanical treatment, and burning (Pellant 1990; Mosley 1996; Whisenant 1999), the use of livestock as a biological control may provide an effective and less expensive alternative or supplement to these methods. Livestock such as cattle and sheep would be readily available in the Intermountain West, and the utilization of cheatgrass as forage could help offset cheatgrass control costs as well as benefit local ranchers.

However, there is uncertainty as to the level of control that could be obtained using this method. Cheatgrass has flourished despite being used widely as a forage grass in the Intermountain West (Klemmedson and Smith 1964). Indeed, the rapid and widespread invasion of cheatgrass has largely been attributed to overgrazing and dispersal by livestock, as native perennial grasses are more susceptible to grazing damage than cheatgrass (Miller et al. 1994). While perennial grasses in this region are highly susceptible to damage from grazing when the inflorescences are elevated (Booysen et al. 1963, Olson and Richards 1988), cheatgrass, like other weedy species, may possess traits that will facilitate its recovery following defoliation. In a more mesic environment, inflorescence production of non-native grasses was found to increase after two years of defoliation by mowing (Clark and Wilson 2001). Briske (1986) classified grazing avoidance and tolerance as the two mechanisms by which plants are able to survive grazing. Tolerance includes morphological and physiological traits that allow a plant to produce new growth following defoliation. Avoidance includes morphological and biochemical traits that allow a plant to escape defoliation. For instance, grazing tolerance can occur in plants that have asynchronous tiller development, in which a plant's tillers may occur at different stages of development. Following removal of the most developed or tallest tillers, less developed or shorter tillers may remain and continue in their development (Richards 1993). Grazing tolerant plants may also be able to rapidly produce and develop new tillers upon removal of the inflorescence, possibly through compensatory growth or existing carbon reserves (Laude 1957; Richards 1986). Grazing avoidance can occur via decumbent growth, in which angular stem growth allows a plant to be missed by the grazing animal (Westoby 1980). Cheatgrass can exhibit both asynchronous tiller development (Harris 1967), and produce decumbent tillers (Young and Evans 1985), which would facilitate grazing tolerance and avoidance, respectively.

In spite of the apparent resilience of cheatgrass under grazing pressure, empirical observations that heavy spring grazing practically eliminated dense stands of cheatgrass provided early evidence that grazing could be used to suppress cheatgrass growth and seed production (Daubenmire 1940; Mosley 1996). Further evidence includes experimental studies that examined the effects of clipping or mowing treatments on cheatgrass growth. In most cases, cheatgrass defoliation late in the spring was found to cause reductions in plant density and biomass in the same or subsequent year (Hulbert 1955; Finnerty and Klingman 1962; Tausch et al. 1994). In a greenhouse study with a steady water supply, cheatgrass biomass and seed production decreased in response to increased grazing intensity by small mammals (Pyke 1986). Field studies have also shown that grazing by small mammals causes at least some annual mortality (Mack and Pyke 1984).

Thus, there is ample evidence from the literature that defoliation can reduce cheatgrass productivity and seed production. There is no direct experimental evidence, however, as to what type of grazing treatments, if any, would be capable of completely preventing or at least severely reducing cheatgrass seed production. Therefore, the first of the primary objectives of this study was to compare the effectiveness of various defoliation treatments in reducing cheatgrass seed production in cheatgrass-dominated areas. This objective was addressed by applying a series of different cheatgrass-clipping treatments. To analyze the effect of each clipping, we asked the following research questions: whether any of the treatments prevented seed production; whether any of the treatments reduced seed production relative to natural levels or relative to other treatments; and whether viable seeds were present when treatments were applied. The response variable for the first three questions was end of season viable seed production (seeds/m^2) (hereafter referred to as seed production) and mid-season viable seed production (seeds/m^2 per clipping event) (hereafter referred to as mid-season seed production) for the fourth question.

Second of the primary objectives was to determine the biological and/or environmental mechanisms by which seed reduction or plant recovery occur. To address this objective, we asked whether any of the treatments caused a reduction in the mechanistic response variable relative to natural levels or other treatments. Biological mechanistic response variables included end of season flowering plant density (plants/m^2) (hereafter referred to as plant density), plant seed production (seeds/plant), and tiller production (percentage of plants with > 1 flowering tiller), while the environmental mechanistic response variable was seasonal volumetric soil moisture (%).

Secondary objectives were to analyze the treatments to assess the immediate effectiveness of the application, and to consider cheatgrass forage production from each treatment as a factor in the feasibility of using livestock as the defoliating agents. To address the first of these, we asked whether the treatment applications were successfully timed to coincide with the appropriate plant phenologies, and whether the treatments were able to remove the majority of cheatgrass inflorescences. The analyzed response variables were plant phenological status (%) and inflorescences removed (%). To consider cheatgrass as forage for livestock, we asked how much cheatgrass dry biomass was removed by each treatment, and how many cow-calf pairs or sheep could be supported by the removed biomass. Response variables included cheatgrass dry biomass removed (g/m^2 and %) (hereafter referred to as cheatgrass biomass), and cattle and sheep stocking rates (number of cow-calf pairs or sheep/hectare*day).

Materials and Methods

Site Description

Experiments occurred at Lincoln Bench (Lincoln Bench) (43°54'25"N, -117°9'27"W) and Succor Creek (Succor Creek) (43°34'5"N, -117°6'20"W) — two, four-acre sites in Malheur County of eastern Oregon (Appendix A, Figure 1). Both sites were dominated by cheatgrass and located in western Intermountain sagebrush steppe (West 1983). At both sites, cheatgrass made up greater than 60% of the vegetative cover, with native perennial grasses representing less than 1% (see Appendix A, Figures 2A and 2B for photographs). Both sites included the principle native plants, Sandberg bluegrass (*Poa secunda* J. Presl) and small fescue (*Vulpia microstachys* (Nutt.) Munro). Prominent exotic species at Lincoln Bench included bulbous bluegrass (*Poa bulbosa* L.) and redstem stork's bill (*Erodium cicutarium* (L.) L'Hér. Ex Ait.), and at Succor Creek included tall tumble-mustard (*Sisymbrium altissimum* L.), redstem stork's bill, curveseed butterwort (*Ranunculus testiculatus* (Crantz) Bess.), annual wheatgrass (*Eremopyrum triticeum* (Gaertn.) Nevski), and bulbous bluegrass (taxonomic nomenclature follows USDA NRCS 2004).

Site locations were recommended by the Bureau of Land Management (BLM) Vale District Office to provide a range of precipitation typical of Wyoming big sagebrush (*Artemesia tridentata* Nutt. ssp *wyomingensis* Beetle and Young) communities in the Intermountain West. At 927 m, the Lincoln Bench site was selected as the more mesic site, with an estimated mean annual precipitation of 28.5 cm/year. At 824 m, Succor Creek was selected as the more xeric site, with an estimated mean annual precipitation of 24.9 cm/year. Mean annual precipitation estimates were made using PRISM, a climate mapping system that incorporates a spatial climate knowledge base (Spatial Climate Analysis Service 2004). Estimated precipitation for the year of the study based on PRISM estimates (September 2002 – August 2003) was approximately 24.1 cm and 21.8 cm at Lincoln Bench and Succor Creek, respectively. Both sites experienced relatively low amounts of precipitation—about 85% of the historical average— during the study, with below average precipitation occurring in autumn 2002 and early spring 2003, periods of potentially high cheatgrass germination and growth (Figure 1).

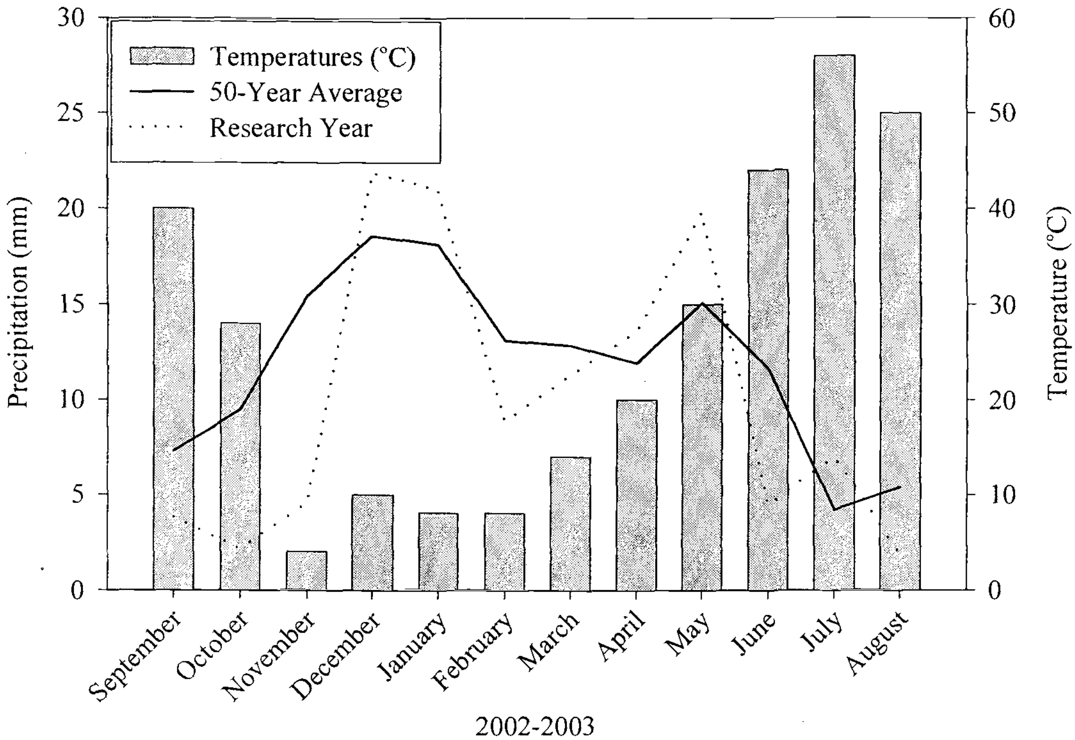

Figure 1. Climatic diagram for Lincoln Bench. Monthly precipitation for September 2002 – August 2003 estimated using PRISM data. Temperature monthly means estimated using on-site recorders (September-November estimates are from 2003) (HOBO ProSeries Temp, Onset). Succor Creek data are not shown but had a similar pattern.

No published soil surveys were available for this region of Malheur County. Basic soil descriptions were completed for each site in June of 2003. Lincoln Bench soils were characterized as a non-sticky, slightly plastic silty clay loam to 11 cm, and a slightly sticky, moderately plastic silty clay from 11 to 44 cm. Succor Creek soils were characterized as a slightly sticky, very plastic silty clay loam to 5 cm., and a slightly sticky, very plastic silty clay to 50 cm. (See Appendix B for more complete soil descriptions).

Average volumetric soil moisture was measured using a time-domain reflectometer (Trase 2100 TDR, SoilMoisture Equipment Corporation) by vertically inserting 30-cm probes in the soil of the buffer of each treatment in three randomly chosen blocks during late April 2003. Soil moisture readings were taken weekly during the experiment from April 26 to May 25, 2003, and again on June 8, 2003. Values were averaged across blocks and dates for a seasonal site average. On average, soil volumetric water content over the three months was 10.3% (95% CI = 9.4 - 11.3%) for Lincoln Bench, and 12.0% (95% CI = 11.0 – 13.1%) for Succor Creek. Other than an early May increase in Lincoln Bench soil moisture, Succor Creek soil moisture appeared to be

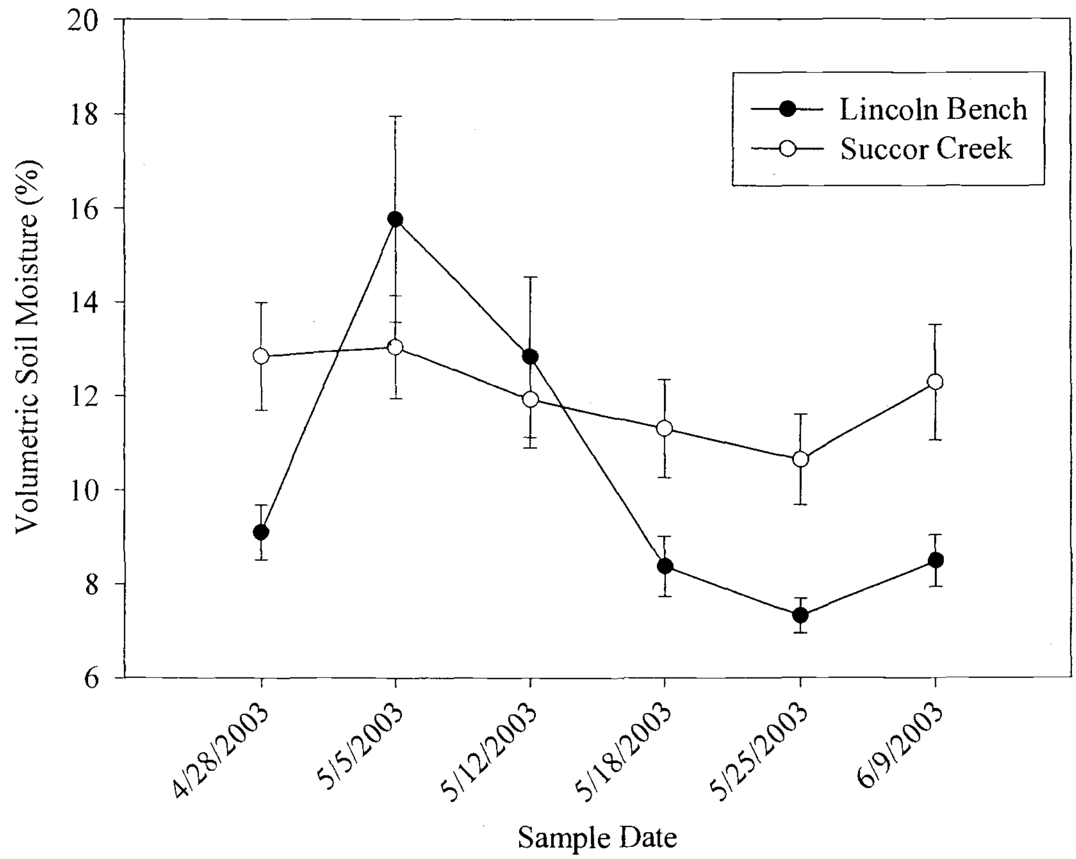

Figure 2. Weekly volumetric soil moisture for Lincoln Bench (solid circles) and Succor Creek (open circles) for the duration of the experiment. Error bars indicate 95% confidence intervals.

higher and less variable for most of the growing season (Figure 2). Higher soil moisture levels could occur at Succor Creek despite similar precipitation values if differences in soil characteristics allow greater moisture retention or if site transpiration rates were lower.

Experimental Design

Experimental treatments were combined in a factorial arrangement and included clipping of cheatgrass at the onset of two phenological stages (Boot (B) and Purple (P) stages), two clipping heights (Short (S) = 2.5 cm; Tall (T) = 7.6 cm), two clipping frequencies (once (1) and twice (2)), and a control of no clipping (C). The boot stage was defined as the moment when inflorescences were just beginning to emerge from the sheath, but were not fully extended. This stage marks the moment that plants start to become most susceptible to grazing since the apical meristem is elevated. The purple stage was defined as the moment at which caryopses and/or glumes turned a red or purple color, which roughly corresponds to the 'dough' stage referred to in the literature (Hulbert 1955). The purple stage marks the moment that plants start to become less palatable to livestock (Klemmedson and Smith 1964). Using these two stages, we were able to examine the effect of defoliation on cheatgrass during early and late-season flower production. Both stages are also easily recognizable in the field.

Clipping heights were chosen to reflect heights to which livestock might graze plants. The taller height of 7.6 cm was chosen to test the recommendation by Mosley (1996) that cheatgrass can be controlled by grazing to at least this height with sheep, even though sheep are capable of grazing cheatgrass to about 1.0 cm (Cook and Harris 1952). Cattle should be able to graze cheatgrass plants to about 2.5 cm (Pellant pers. comm.), which was consequently chosen as our second height. Second clippings were conducted to account for potential regrowth through tiller development, and were also recommended by Mosley (1996).

Clippings occurred when the tallest stems of the majority of plants in treatment plots were at the appropriate phenological stage. Sites were monitored closely throughout the season, and surveys were conducted to determine cheatgrass plant phenological status immediately before treatments were applied. Phenology surveys were completed within four, 39-cm^2 quadrats placed randomly within each plot. Proportions of plants in each phenological stage were averaged across the four-quadrat subsamples. As seeds matured and began to drop, about one week after the purple stage clippings, a second clipping of purple treatments was not practical and was not done. Thus, there were a total of seven treatments labeled according to clipping height, phenology of the plant at the time of clipping, and clipping frequency (Table 1).

Table 1. Clipping treatments and corresponding codes in which "Short" = 2.5 cm and "Tall" = 7.6 cm.

Treatment (Clipping Height, Phenologic Stage, and Frequency)	Code
Short Boot Once	SB1
Short Boot Twice	SB2
Tall Boot Once	TB1
Tall Boot Twice	TB2
Short Purple	SP
Tall Purple	TP
Control	C

All treatments were located in nine blocks using a randomized complete block design to allow for observed variation in plant density across research areas. Each experimental unit consisted of a 1-m^2 treatment area surrounded by a 1-m buffer, for a total area of 9 m^2. Blocks were 9 by 9-m consisting of 9 potential treatment plots (two randomly selected plots were not used). Blocks falling on areas with extremely low cheatgrass density were not used and new blocks were randomly selected.

The short and tall boot clippings occurred on April 26 and May 10, 2003. Short and tall purple clippings occurred on May 24, 2003. The experiment was terminated and samples harvested one week after the purple clipping (during the week of June 2) when seeds were mature and had just begun to disperse. Thus, the entire experiment lasted five weeks, approximately spanning the period of cheatgrass development from the boot stage to seed dispersal.

Clipping treatments were conducted by cutting all plants in the 1-m^2 treatment plot with scissors. Plants were clipped at 2.5 or 7.6 cm using a small wooden guide with a wire marking the appropriate height. All plant mass clipped inside the treatment area was bagged and labeled by plot. To quantify the proportion of cheatgrass defoliated and removed in each treatment, eight randomly selected individual cheatgrass plants in the buffer zone of the experimental unit were clipped at the same height as in the treatment plot and at ground level. Both portions were bagged and labeled separately, dried, and weighed. The remaining plants in the buffer were clipped to approximately the same height as the inner treatment plot using either a mower or by hand with scissors, as determined by topography and rockiness of the plot. Clipped plant matter in the buffer area was removed and discarded to prevent dispersal of seed and other plant material into treatment areas. The effectiveness of each clipping treatment in removing cheatgrass inflorescences was determined by calculating the proportion of cheatgrass plants deheaded. These surveys for inflorescences removed were done one week following treatment applications.

Plants and litter were sampled from all plots during the week of June 2 to measure seed production, plant density, and tiller production. Litter samples were included for estimates of seed production since some seed had already dropped at the time of harvest. All living plants (i.e. plants that still had an inflorescence at the end of the season) were clipped to ground level in the center 0.25-m^2 area of each treatment plot and collected in labeled paper bags. Litter samples were collected by randomly placing a 0.01-m^2 quadrat at two locations inside the same 0.25-m^2 area after plants had been removed.

Sample Processing

For end of season seed production (seeds/m^2), seeds were stripped from plants by hand and stored separately for each plot. Seeds were separated from litter samples using a screen. The resulting seed samples were then further cleaned of chaff and empty florets by running them through a pneumatic scarifier (Hoffman Manufacturing) at 25 psi for approximately one minute per gram of seed. Preliminary tests showed that this cleaning procedure had no effect on cheatgrass seed germination (unpublished data). To get a seed count for all samples with greater than 200 seeds, an average seed weight (grams/seed) was calculated using random subsamples of seed. Total seed weight per plot was divided by the average seed weight to estimate seed number. Since a maximum of 200 seeds was used in germination tests (see below), seeds from samples with equal to or fewer than 200 seeds were counted directly. Plant seed production was calculated using end of season seed production estimates divided by plant density of the same treatment plot (see below).

For mid-season seed production estimates (seeds/m^2) for each of the three clipping events, the same protocols were followed except that plant samples from only three randomly chosen blocks at each site were processed due to time constraints. Seeds were also stripped by hand from all plant material clipped within the 1.0-m^2 treatment plot, and no further cleaning was done.

Seed germinability and viability of plant and litter samples were estimated using germination tests in October 2003, approximately four months after collection. Two hundred seeds (intact caryopsis with or without the lemma and palea) were randomly selected from each sample and divided into subsamples of 50, which were each placed in one of four petri dishes on germination paper (Association of Official Seed Analysts (AOSA) 2002a). If a sample had fewer than 200 seeds, all seeds were used, with a maximum of 50 seeds to a dish. Germination paper was saturated with distilled water and dishes were covered, randomly placed in a growth chamber, and incubated for 10 days at 25°C, with dishes remoistened as needed. Ten days at 25°C was deemed adequate for complete germination of cheatgrass seeds during preliminary tests (unpublished data). Cheatgrass seedlings per dish were then counted according to the AOSA (2002b) rules for seedling evaluation. Seeds were considered germinated when a seedling developed a root and shoot, with the shoot located at least halfway up the hypocotyl. Abnormal seedlings, seeds infested with fungus, and ungerminated seeds were considered non-viable. Non-germinated seeds were tested for viability using tetrazolium chloride when dishes had less than 60% germination. A negligible number of non-germinated seeds were found to be viable from these tests, which corresponds with findings that cheatgrass seeds often achieve 100% germination following an after-ripening period of four months (and therefore have no further dormancy that would require TZ testing for viability) (Beckstead et al. 1993; Pyke and Novak 1994).

For samples with greater than 200 seeds, the percentage of germinated seeds was averaged across the four subsamples for an estimated germination percentage for that sample. For samples with less than 200 seeds, the actual germination percentage of that sample was used for the entire treatment. Germination percentages were then multiplied by the estimated seed numbers to determine the number of viable seeds per sample. Plant and litter viable seed totals were then summed to estimate the number of viable seeds/m^2 for each plot.

Plant density (plants/m^2) and tiller production (percentage of plants with > 1 flowering stem) were determined by counting individual flowering plants and the number of flowering tillers per plant. The percentage of plants with greater than one flowering stem was then calculated for lateral flowering tiller production. Plants infested with smut (*Ustilago bullata*) were not stripped of seed, and were not included in plant density or tiller production values because these plants rarely produce viable seeds and the fungus can increase the number of tillers produced by plants (Fisher and Holton 1957, Falloon 1979, Pyke 1983).

Cheatgrass biomass (g/m^2) was estimated by oven-drying the clipped plant matter taken from each treatment plot during each application at 50°C for 72 hours and weighed. Seed weights from the matching treatment in the three blocks used in estimating seed numbers (see above) were added to these samples for total production.

The proportion of cheatgrass biomass removed by clipping was determined using buffer samples. Weights of the clipped portion of the plant along with the whole plant were used. The proportion clipped was calculated by dividing the clipped weight by the whole plant weight.

Livestock stocking rates (cow-calf pairs/day*ha) (sheep/day*ha) were determined by extrapolating cheatgrass biomass estimates from each clipping event to kg/hectare, and dividing this number by the estimated daily forage requirement for a cow-calf pair and a single sheep. Approximately 385.55 kg/month (or 12.85 kg/day) are required for a cow-calf pair, and approximately 77.11 kg/month (or 2.57 kg/day) for one sheep (Sheley et al. 2003).

Statistical Analyses

Means and 95% confidence intervals were calculated for plant phenological status, inflorescences removed, mid-season seed production, cheatgrass biomass, and livestock stocking rates. Analysis of Variance (ANOVA) (Proc Mixed; SAS 1999) was used to test the null hypotheses of no difference in cheatgrass seed production, plant density, plant seed production, tiller production, and volumetric soil moisture among treatments, including the control. Although multiple response variables were analyzed, a Multiple Analysis of Variance (MANOVA) was deemed inappropriate either because response variables were not correlated, or because evaluating response values of correlated variables was of primary interest rather than their relative influences on treatment differences (Huberty and Morris 1989; Ramsey and Schafer 1997; Scheiner 2001). At Succor Creek, plant density was evaluated with an Analysis of Covariance with initial density as a covariant, since there was evidence of a strong correlation between initial and final plant density ($r^2 = 0.62$, $p<0.001$) (Proc Corr; SAS 1999). Depending on the results of the ANOVA and ANCOVA tests, all pair-wise comparisons were made between treatments using the Tukey-Kramer adjustment for multiple comparisons, since a greater number of comparisons were made than were treatment degrees of freedom. The significance level was set at 0.05.

All variables were assessed for normality and equal variance before analysis. Residual plots showed equal variance for tiller production at Succor Creek, but suggested the need for a transformation for seed production, plant density, and plant seed production at both sites, and for volumetric soil moisture at Lincoln Bench. For each of these variables, the equal variance assumption was met using a log transformation (Appendix C, Figures 1A to H). Therefore, the back-transformed means and 95% confidence intervals were calculated and reported. Normality was deemed adequate for these response variables at both sites (Appendix C, Figures 2A to H). A transformation could not be found that would adequately equalize the variance for tiller production at Lincoln Bench, nor for soil moisture at Succor Creek. Therefore, only means and 95% confidence intervals were calculated and reported for these two variables.

Results

Plant Phenological Status

The phenology survey indicates that first boot and purple clippings occurred when the majority of plants were at the appropriate phenological stages (Figures 3A and B).

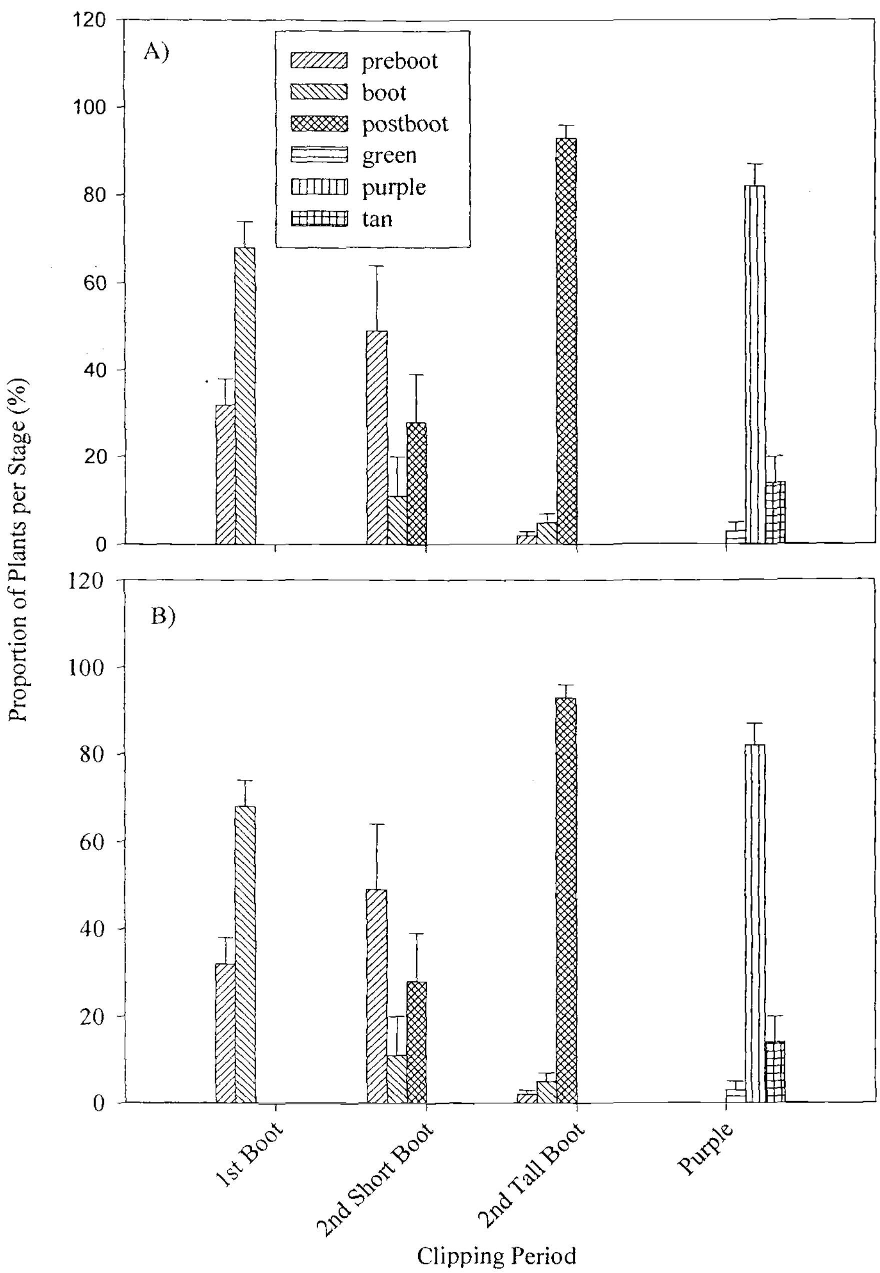

Figure 3. Distribution of cheatgrass phenologies within populations during each clipping period at A) Lincoln Bench and B) Succor Creek. Error bars indicate 95% confidence intervals.

Notably, a large proportion of plants at different stages were present as well, including the preboot stage during the first boot clippings, and plants that had senesced (turned a tan color) during the purple clipping.

Inflorescences Removed

Short clipping treatments tended to remove a greater proportion of inflorescences at both sites than tall treatments, although no treatments could apparently remove 100% of the inflorescences (Figure 4). Within a removal height treatment, the later

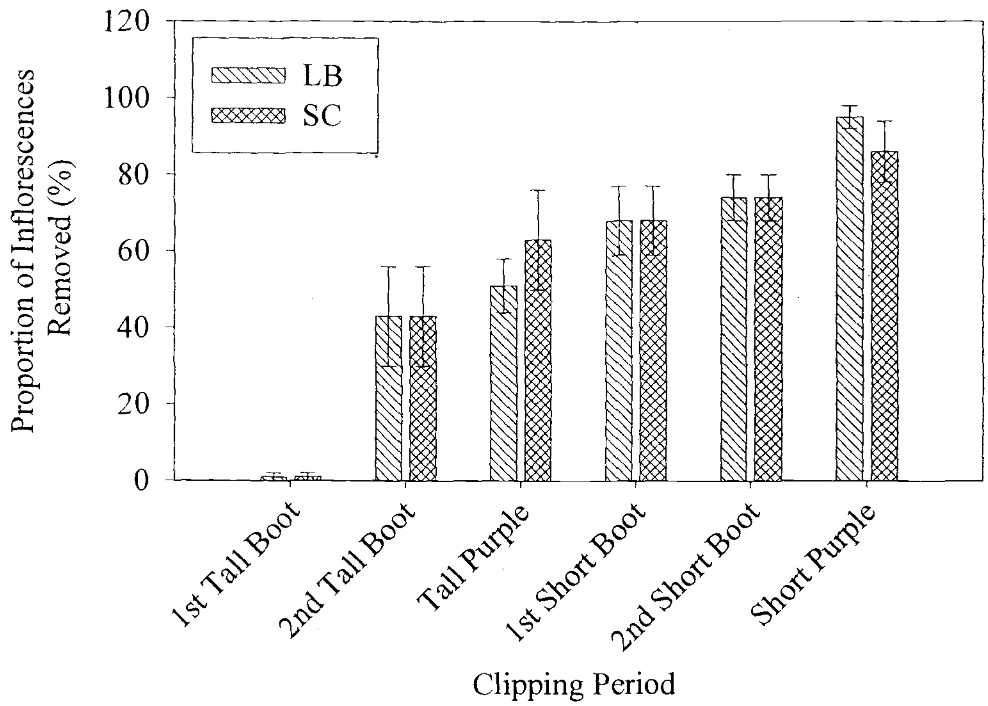

Figure 4. Estimates of proportion of cheatgrass inflorescences removed by clipping treatments at Lincoln Bench and Succor Creek. Error bars indicate 95% confidence intervals.

phenological or purple stage tended to remove the most inflorescences while the earlier boot stage removed the least.

Seed Production

Seed production was greater than zero for all treatments, and the effect of clipping on seed production differed significantly among treatments at both Lincoln Bench ($F_{6,43}$ = 43.64, p< 0.0001) and Succor Creek ($F_{6,41}$=20.14, p<0.0001) (Figure 5). At Lincoln

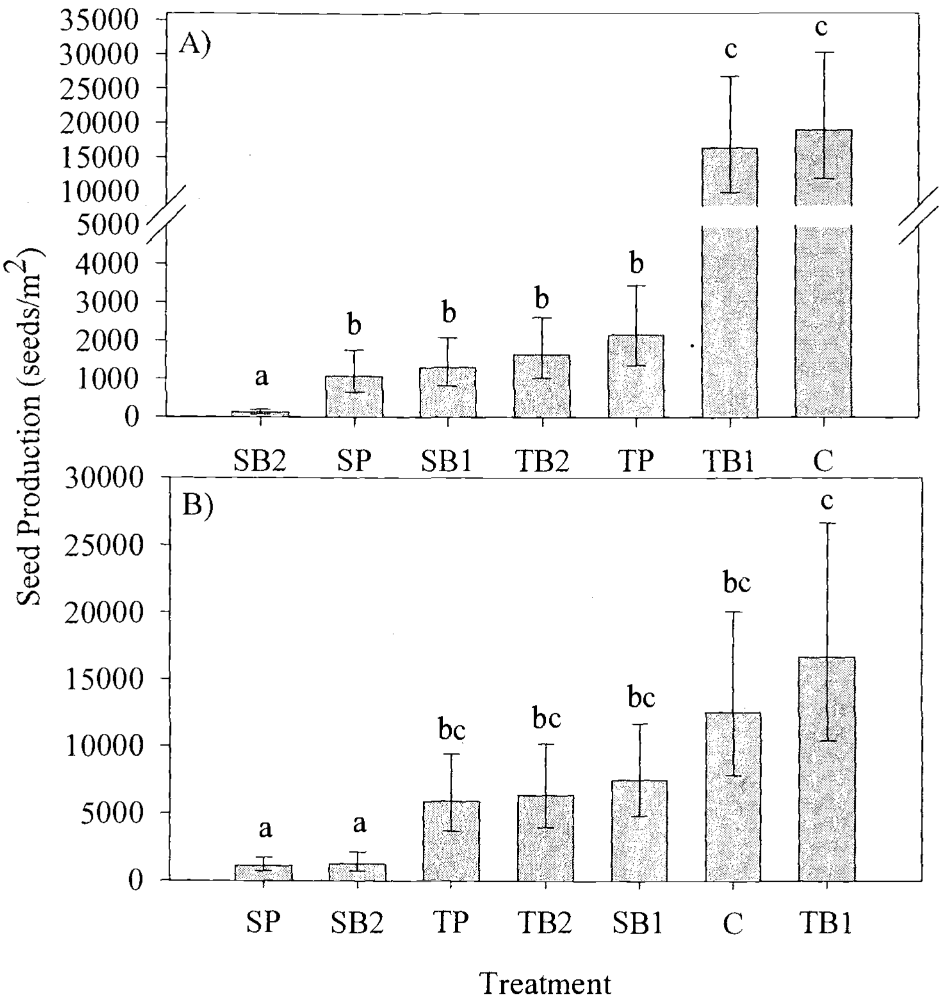

Figure 5. Estimates of back-transformed mean end of season cheatgrass seed production at A) Lincoln Bench and B) Succor Creek. Error bars indicate 95% confidence intervals. Estimates with the same letters are not significantly different at the 0.05 level. See Table 1 for definitions of treatment abbreviations.

Bench, all treatments except the TB1 treatment were significantly less than the control, while at Succor Creek, only SB2 and SP were significantly less than the control. The SB2 treatment had the lowest seed production value at Lincoln Bench, with approximately a 99% reduction relative to the control. Both SB2 and SP had the lowest seed production values at Succor Creek, with approximately a 95% reduction relative to the control. Overall, the short clippings at the middle and end of the season were the most effective in reducing cheatgrass seed production, while the tall clippings at the middle and end of the season and the short clipping early in the season had intermediate levels of reduction. The tall treatment clipped early in the season had no effect on seed production.

Mid-Season Seed Production

Viable seeds were produced rarely in clipping treatments earlier in the season, with their occurrence limited to the time of the second round of boot clippings. At this time, average seed viability was approximately 33 to 58% at Succor Creek and Lincoln Bench, respectively, with a maximum production of about 24 seeds/m^2 at Lincoln Bench TB2 plots. Viable seeds were clearly present at the time of the purple clippings with average viability of 92 and 97% at Succor Creek and Lincoln Bench, respectively, resulting in about than 3,211 seeds/m^2 at Succor Creek and 10,643 seeds/m^2 at Lincoln Bench.

Plant Density, Plant Seed Production, and Tiller Production

Some clipping treatments led to significant reductions in plant density ($F_{6,48}$=29.95, p<0.0001 (Lincoln Bench); $F_{6,44}$=20.37, p<0.0001 (Succor Creek)) and plant seed production ($F_{6,43}$=25.14, p<0.0001 (Lincoln Bench); $F_{6,41}$=3.74, p=0.0046 (Succor Creek)) at both sites, and in tiller production at Succor Creek ($F_{5,37}$=8.41, p<0.0001). Plant density followed a response pattern similar to that for seed production. At Lincoln Bench, plant density decreased relative to the control for short clippings and the TP clipping, with SP and SB2 clippings having the lowest plant density (Figure 6).

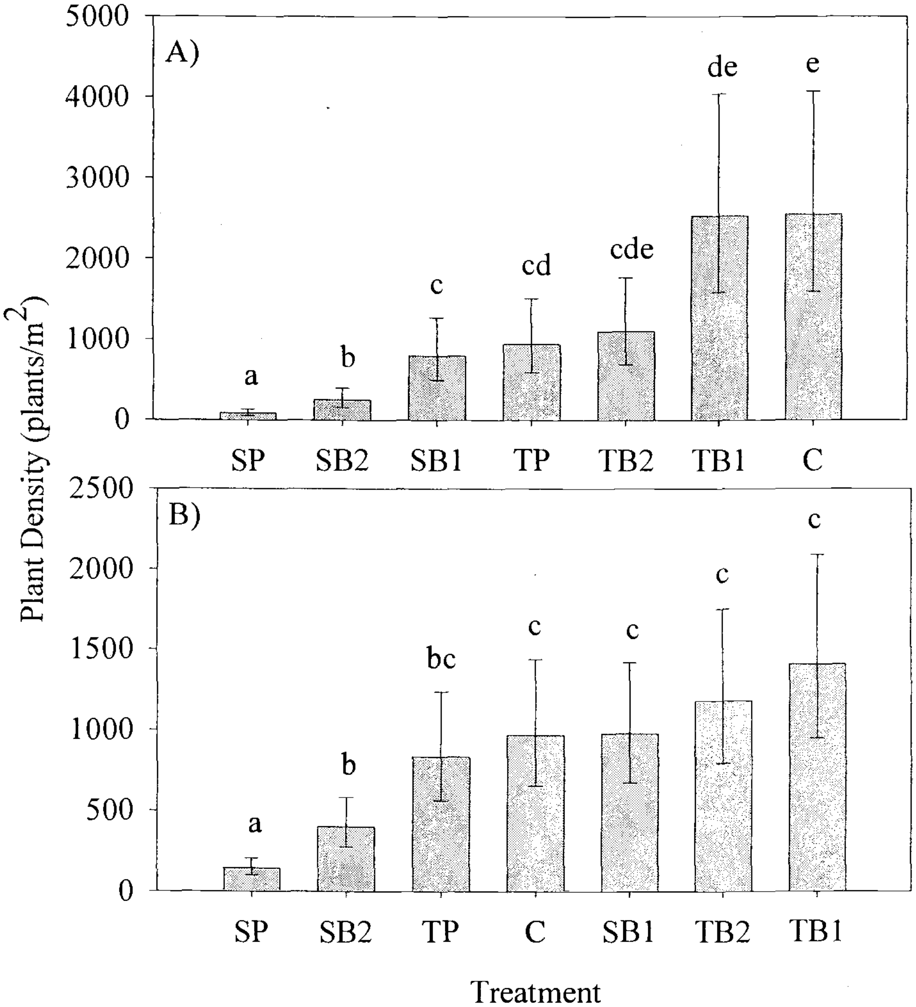

Figure 6. Estimates of back-transformed mean end of season cheatgrass plant density at A) Lincoln Bench and B) Succor Creek. Error bars indicate 95% confidence intervals. Estimates with the same letters are not significantly different at the 0.05 level. See Table 1 for definitions of treatment abbreviations.

At Succor Creek, only the two short clippings that occurred later in the growing season (SB2 and SP) decreased plant density relative to the control (Figure 6). At Lincoln Bench, plant seed production followed a response pattern similar to plant density, excluding the SP treatment—which did not decrease relative to the control (Figure 7).

This was also true at Succor Creek, where the SB2 and TB2 treatments decreased relative to the control, but not the SP treatment (Figure 7).

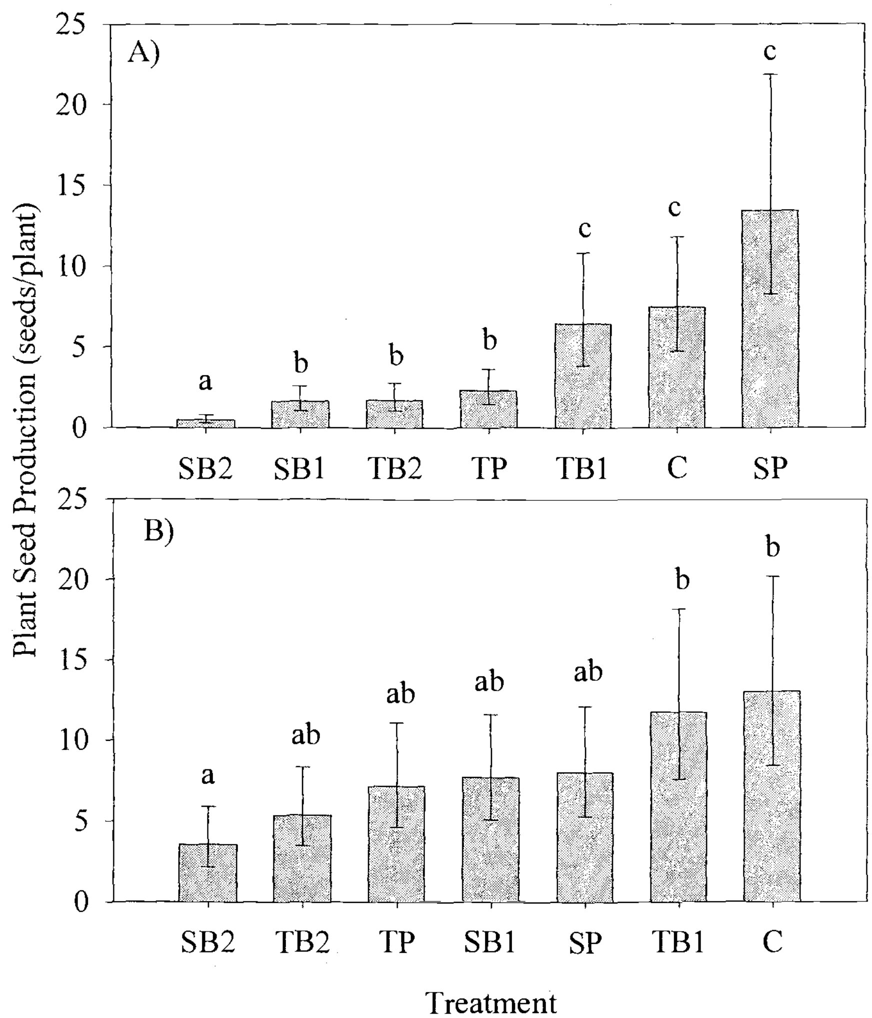

Figure 7. Estimates of back-transformed mean end of season cheatgrass plant seed production at A) Lincoln Bench and B) Succor Creek. Error bars indicate 95% confidence intervals. Estimates with the same letters are not significantly different at the 0.05 level. See Table 1 for definitions of treatment abbreviations.

Tiller production in the SB1 treatment at Succor Creek increased significantly ($p<0.01$) relative to the control, with a percentage of plants with greater than one flowering stem 7.4 times greater than that of the control (95% CI = 1.1 to 13.7). Although significance could not be tested, Lincoln Bench data suggested a similar pattern of tiller production for the SB1 as well as the SB2 treatment, with 3.0% (95% CI = 1.6 –

4.4%) and 10.1% (95% CI = 6.2 – 14.0%) of plants with greater than one flowering stem, respectively, versus 0.2% (95% CI = 0.0 – 0.4%) for the control. Decumbent tillers were documented in the harvest samples at Succor Creek in four of the nine SB1 treatment replicates, as well as in a TB2, TP1, and C replicate. However, plants with decumbent tillers made up no more than 2% of the total plants in these cases, and were not observed in the harvest samples at Lincoln Bench.

Soil Moisture

An ANOVA found no evidence of an effect of treatment on seasonal volumetric soil moisture at Lincoln Bench ($F_{6,12}$ = 1.21, p= 0.3659). However, some variability in seasonal volumetric soil moisture associated with treatments was suggested by the Lincoln Bench data, with the treatment plots tending to have lower values than the control plots (Figure 8). Succor Creek mean seasonal volumetric soil moisture values appeared more consistent among treatments (Figure 9). However, the possible variability

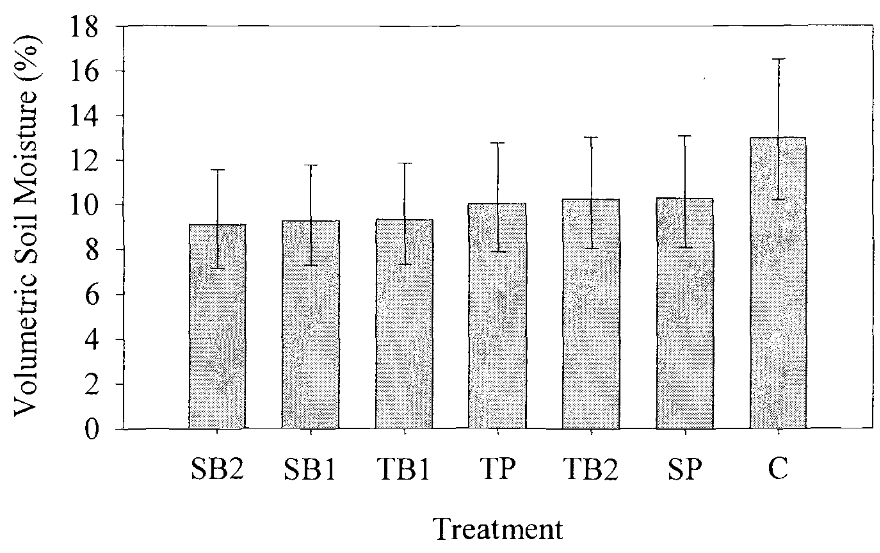

Figure 8. Estimates of back-transformed mean seasonal volumetric soil moisture at Lincoln Bench. Error bars indicate 95% confidence intervals. See Table 1 for definitions of treatment abbreviations.

seen at Lincoln Bench might warrant further investigations with a larger sample size to increase statistical power.

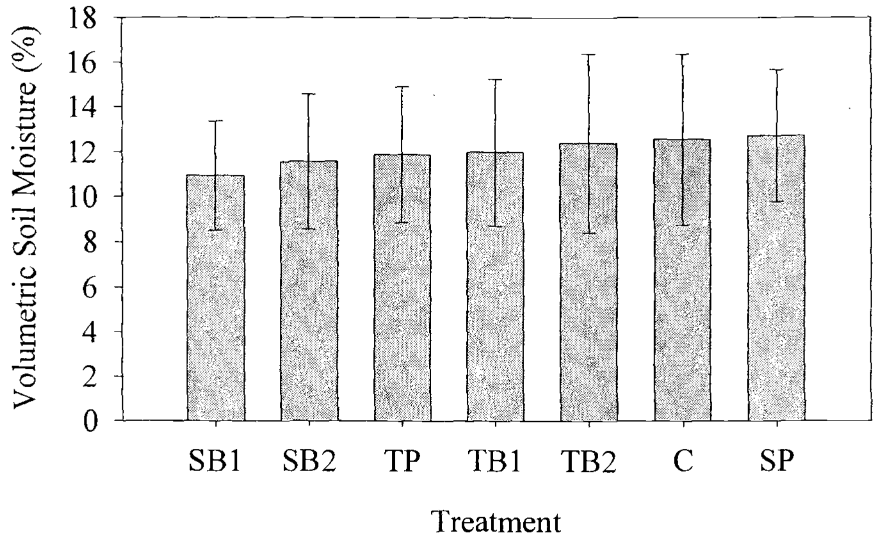

Figure 9. Estimates of mean seasonal volumetric soil moisture at Succor Creek. Error bars indicate 95% confidence intervals. See Table 1 for definitions of treatment abbreviations.

Cheatgrass Forage Production

The largest amount of cheatgrass biomass removed by a clipping treatment was about 100 times larger than the smallest amount at both sites. The TB2 treatment consistently had the least foliage removed, while one of the two purple treatments had the most removed (Table 2). These patterns are similar for the proportion of foliage removed (Table 3). According to estimates of livestock stocking rates obtained by converting cheatgrass production into animal units, all but the TB1 clippings should be able to support at least 7 cow-calf pairs or 14 sheep per acre per day at both sites (Tables 4A and 4B).

Table 2. Estimated mean dry biomass of cheatgrass removed during each treatment period. See Table 1 for definitions of treatment abbreviations.

	Lincoln Bench		Succor Creek	
Treatment	Biomass (%)	95 % CI	Biomass (%)	95 % CI
SB1	36.5	29.5 - 43.4	11.7	6.6 - 16.7
TB1	1.6	0.3 - 2.9	1.2	0.3 - 2.2
1st SB2	30.7	24.2 - 37.2	9.1	4.4 - 13.9
2nd SB2	9.4	4.8 - 13.9	9.2	6.9 - 11.5
1st TB2	1.2	0.3 - 2.0	0.8	0.2 - 1.4
2nd TB2	37.5	28.0 - 47.0	15.9	8.6 - 23.3
SP	103.7	81.5 - 126.0	29.5	18.8 - 40.3
TP	62.1	46.3 - 77.9	45.4	33.8 - 57.0

Table 3. Estimated mean proportion of dry biomass of cheatgrass removed during each treatment period. See Table 1 for definitions of treatment abbreviations.

	Lincoln Bench		Succor Creek	
Treatment	Biomass (%)	95 % CI	Biomass (%)	95 % CI
SB1	50.3	31.5 - 69.1	40.8	31.0 - 50.6
TB1	1.5	0.2 - 2.8	2.1	0.9 - 3.3
1st SB2	43.9	33.1 - 54.7	31.2	10.4 - 51.9
2nd SB2	47.3	39.1 - 55.4	44.6	35.2 - 54.0
1st TB2	0.9	0.3 - 1.5	4.3	1.4 - 7.1
2nd TB2	31.2	23.8 - 38.5	24.4	13.8 - 35.1
SP	73.3	70.9 - 75.8	74.6	71.2 - 78.1
TP	44.8	39.5 - 50.1	50.7	42.4 - 59.1

Table 4. Estimated mean number of A) cow-calf pairs per hectare based on a forage requirement of 12.85 kg/day and B) sheep based on a forage requirement of 2.57 kg/day. See Table 1 for definitions of treatment abbreviations.

A) Cow-calf	Lincoln Bench		Succor Creek	
Treatment	Cow-calf pairs /day*hectare	95% CI	Cow-calf pairs /day*hectare	95% CI
SB1	29.2	23.6 - 34.8	9.3	5.3 - 13.5
TB1	1.3	.3 - 2.3	1.0	0.3 - 1.8
1st SB2	24.5	19.3 - 29.7	7.3	3.6 - 11.2
2nd SB2	7.5	3.8 - 11.2	7.4	5.6 - 9.1
1st TB2	0.9	.3 - 1.5	0.7	0.3 - 1.3
2nd TB2	30.0	22.4 - 37.6	12.7	6.9 - 18.5
SP	83.0	65.3 - 100.8	23.6	15.0 - 32.3
TP	49.7	37.1 - 62.2	36.3	26.9 - 45.5

Forage requirement = 12.85 kg/day

B) Sheep	Lincoln Bench		Succor Creek	
Treatment	Sheep/day* hectare	95% CI	Sheep/day* hectare	95% CI
SB1	57.4	46.4 - 68.3	18.3	10.3 - 26.3
TB1	2.5	0.5 - 4.6	1.9	0.5 - 3.4
1st SB2	48.3	38.1 - 58.5	14.4	6.9 - 21.9
2nd SB2	14.7	7.6 - 21.8	14.5	10.9 - 18.1
1st TB2	1.8	0.5 - 3.2	1.3	0.4 - 2.2
2nd TB2	59.0	44.0 - 73.9	25.1	13.5 - 36.6
SP	163.2	128.2 - 198.2	46.5	29.6 - 63.4
TP	97.7	72.9 - 122.6	71.4	53.2 - 89.6

Forage requirement = 2.57 kg/day

Discussion

Seed Production

Overall, plants clipped to a height of 7.6 cm and those that were clipped once in the boot stage were less effective in reducing cheatgrass seed production. The most effective defoliation treatment clipped plants twice to a height of 2.5 cm—once when the majority of plants were in the boot stage, and again two weeks later when a majority of plants were in pre-boot and post-boot stages. While this study provides evidence that Mosley's (1996) recommendation for grazing to 7.6 cm is inadequate for cheatgrass control and a shorter defoliation is necessary, it does support his recommendation to graze sheep once in late spring and again when new inflorescences have developed.

The results from Succor Creek indicate that cheatgrass plants clipped to 2.5 cm when the majority of plants were in the purple stage was also effective in reducing seed production. However, a large amount of seed with high viability was also present in plants removed during this clipping treatment. Thus, unless a defoliation treatment can remove 100% of the seed, some of the viable seed will escape during defoliation and contribute to the seed bank. If livestock are being used to control cheatgrass, the viability of seed after passing through the digestive system of livestock should be investigated, since seed from other species, such as "Hycrest" crested wheatgrass (*Agropyron desertorum* (Fisch. Ex Link) Schult. X *A. cristatum* (L.) Gaert.), has been found to survive digestion (Auman et al. 1998). Furthermore, cheatgrass seeds began to harden during the purple stage, creating a greater risk of injury to livestock if cheatgrass is grazed this late in the season (Mosley 1996). Along with the greater seed production, a substantial proportion of plants had already senesced, which decreases cheatgrass palatability and nutritive value (Klemmedson and Smith 1964), meaning livestock grazing efficiency might be reduced with little or no benefit to livestock growth.

Conversely, there was very little seed produced earlier in the season during either boot stage clipping, and the seed that was produced during the second boot clippings had relatively low viability. Thus, there would be a lower risk of seeds dispersing during defoliation if plants were defoliated before entering the purple stage. These results are consistent with other studies examining cheatgrass phenology and the use of prescribed grazing, which generally recommend defoliating cheatgrass before its seed enters the soft "dough" stage (which approximately coincides with the purple stage) to avoid viable seed production (Mosley 1996).

Although the SB2 treatment has the most potential for reducing seed production out of the six treatments tested, plants under the SB2 treatment still about 120 and 1243 seeds/m^2 at the end of the season at Lincoln Bench and Succor Creek, respectively. If the majority of these seeds were to successfully germinate, the SB2 treatment could still result in cheatgrass densities in the range of 100 to 1000 plants/m^2. Whether or not this level of control is adequate for the seedbed preparation of a native reseeding project is uncertain. An observational study by Harris (1967) found that in plots with 90 to 100 cheatgrass plants/m^2, survival of bluebunch wheatgrass seedlings (*Pseudoroegneria spicata* (Pursh) A. Love) was only about 39% (wheatgrass:cheatgrass ratios $\approx$ 1:3) and 69% in plots with about 15 to 20 cheatgrass plants/m^2 (ratios $\approx$ 2:1), versus 86% in plots with 0 to 4 cheatgrass plants/m^2 (ratios $\approx$ 9:1). Historical field trials from 1948 (Hull and Stewart) compared various cheatgrass control methods in conjunction with artificial seedings of a perennial grass mix dominated by crested wheatgrass (*Agropyron cristatum* (L.) Gaertn.), a non-native perennial. Plots retaining less than 100 cheatgrass plants/m^2 the year following treatment tended to have higher crested wheatgrass survival after three years than plots with greater than 100 plants/m^2 (e.g. 21% versus 13% in burned plots, and 12% versus 3% in deeply furrowed plots) (Hull and Stewart 1948). However, there is no statistical evidence indicating whether or not such differences are real, and no controls were carried out to compare survival in plots with no cheatgrass present.

Most cheatgrass competition studies since these early investigations have been greenhouse potted experiments measuring the effect of cheatgrass on native perennial seedling growth rather than survival. However, these studies can still suggest cheatgrass densities that might be detrimental to native seedling survival in artificial seedings in the field. In a greenhouse study, Idaho fescue (*Festuca idahoensis* Elmer) from pristine populations experienced a 35 and 56% decrease in aboveground biomass at fescue:cheatgrass ratios of 1:5 and 1:10, respectively, relative to the control with ratios of 1:0 after 56 days of growth, while Idaho fescue from sites with cheatgrass experienced a 32% decrease at the 1:10 seeding rate (Nasri and Doescher 1995). In a similar study, 'Whitmar' bluebunch wheatgrass growth was negatively impacted after 50 days of growth by a wheatgrass:cheatgrass ratio of 1:4 relative to those of 5:0, 2:0, and 1:0. At this level of competition, bluebunch wheatgrass experienced decreases in leaf development, leaf production (main stem Haun stage), leaf area, tiller production, and shoot dry weight (Aguirre and Johnson 1991). Considering native plants are seeded at rates between about 230 to 300 seeds/m^2 (Ogle 2001), native plant seedlings of a reseeding project would be experiencing competition from cheatgrass in the SB2 treatments of this study at native species:cheatgrass ratios of approximately 2:1 at Lincoln Bench, and 1:5 at Succor Creek, assuming high germination rates. Thus, based on this and historical evidence, there is a chance that in the first year cheatgrass seedling densities could be high enough to reduce the growth and even survival of native seedlings if a reseeding project followed a cheatgrass defoliation treatment similar to the SB2 treatments of this study.

One should also consider the enormous cheatgrass phenotypic plasticity that allows it to exhibit higher per plant seed production at lower plant densities. Young and Evans (1978) found cheatgrass densities to increase from 10 plants/m^2 immediately following a fire to 10,000 plants/m^2 just three years later. This example illustrates how even low densities of cheatgrass have the potential to spread quickly and reestablish dominance in subsequent years, particularly in the absence of mature native perennial plants. Thus, even if native seedlings survived the first year, rapidly escalating cheatgrass densities might still reduce the productivity of young native plants in subsequent years, and so be detrimental to the long-term success of a native plant reseeding project.

More research is needed to determine exactly what cheatgrass densities—and therefore seed production levels—will be acceptable in terms of their impact on both short and long-term native seedling survival and establishment in reseeding projects. Given the evidence that is available, however, and assuming the effects of corresponding grazing treatments will be similar to the clipping treatments of this study, one might predict that even an SB2 grazing treatment might not adequately control cheatgrass population in preparation for native plant reseeding projects. If livestock are used, adjustments needed to make the SB2 treatment more effective may include introducing livestock to the site when the majority of cheatgrass plants are entering the boot stage, and taking them off when plants offsite would be entering the purple stage. This strategy may capture more of the regrowth as well as later developing and shorter plants, and would require maintaining animals on the site for about four weeks based on the phenology observed during this study.

This time period could change, however, depending on available moisture and temperatures. Considering this study was carried out in a relatively dry year, the ability of plants to recover by increasing tiller production and/or maintaining reproduction following defoliation may be improved in a year with greater moisture availability, particularly in the spring (Harris 1967; Richardson et al. 1989). Conversely, an increase in moisture availability could also result in greater plant productivity and height (Klemmedson and Smith 1964), which would make the taller clipping treatments more effective by removing more inflorescences. In this study, cheatgrass plants had often not even reached 7.6 cm in height when clipping treatments were initiated, and many consequently escaped the tall clippings. Furthermore, a year with higher moisture levels may also retard phenological development and thus increase the growing season. This may require a longer or an additional period of grazing depending partly on when additional precipitation occurs.

Despite dry conditions, seed production by control plots in this study was similar to seed production values in similar habitats reported in the literature (Stewart and Hull 1949). In addition, clippings in this study were apparently less effective in causing cheatgrass mortality than similar treatments in other studies (Hulbert 1955; Finnerty and Klingman 1962; Tausch et al. 1994). Although treatment differences could partly explain these variable responses, differing soil moisture and other environmental and biological conditions may also have contributed to the variability, which stresses the importance of considering all factors that could effect cheatgrass survival and seed production from site to site and year to year.

Mechanisms of Seed Reduction

The results of the study indicate that treatments that decreased seed production did so by causing plant mortality and decreased plant reproductive ability. When compared to controls, all treatments that showed a significant decrease in seed production also showed a significant decrease in plant density. In general, treatments with a greater decrease in seed production coincided with those having a greater decrease in plant density, although the decrease in plant density for the SP treatment was the most extreme at both sites. Treatments generally followed the same pattern of response for plant seed production, with the exception of the SP treatment, which did not experience a significant reduction relative to the control at either site. Low plant densities and high plant seed production values for the SP treatment may be explained by a combination of factors. First, as revealed in the post-clipping surveys, the purple treatments experienced the highest removal of flowering tillers. With defoliation occurring so late in the season, plants were unable to produce new tillers—a supposition supported by the tiller production results—and so had a low final flowering plant density. In addition, SP litter seed averaged 88% and 93% of the total seed production at Lincoln Bench and Succor Creek, respectively, while litter seed made up only 38% to 74% of the total seed for the other treatments at both sites (unpublished data). Since plants had already produced high numbers of viable seeds at the time of the purple clippings, high litter seed values may have resulted from some proportion of these viable seeds dropping prior to or during the clipping treatment. If this is the case, these results further strengthen the argument for defoliating prior to the onset of the purple stage.

The substantial proportion of seeds contributed by the litter in all plots also raises the question of whether all litter seed was from the current crop of cheatgrass or was a remnant of the seed bank that had failed to germinate that spring (Pyke 1994; Pyke and Novak 1994). The relatively dry conditions in fall and early spring may have created a situation in which some seed in the litter experienced enforced dormancy. If this is the case, repeating defoliations for more than one growing season might be more effective in depleting the seed bank. Finnerty and Klingman (1962) argued that weed brome grasses could be controlled only by preventing seed production for two years, after which point any seed persisting in the seed bank would be non-viable. Unfortunately, a survey of viable seed in the litter was not carried out prior to seed release in this study. Such information would be helpful in future studies to more completely assess the true effectiveness of defoliation in suppressing seed production.

Mechanisms of Recovery

The results of this study support the premise that cheatgrass resists grazing pressure through both grazing avoidance and tolerance, according to the descriptions by Briske (1986). While short overall plant height made tall clippings less effective overall (short clippings were able to remove approximately 68–95% of the inflorescences, versus about 1–63% by tall clippings), a substantial amount of variability in cheatgrass height and developmental stages were observed in all treatment plots. Indeed, a large proportion of plants was still in the pre-boot stage during the first of the boot clipping treatments. Given adequate moisture, cheatgrass has been noted for its ability to germinate at different times in the fall, winter, and spring—even as late as May—thereby generating different cheatgrass cohorts (Mack and Pyke 1984; Young and Evans 1985). Consequently, the shorter or less developed plants and/or tillers were probably able to avoid defoliation, even in the shorter clipping treatments. Though some plants may simply have been overlooked during the clipping process, these escapees may have accounted for at least some of the flowering tillers observed in surveys the week following treatments, as well as some of the surviving plants surveyed just prior to the second of the boot treatments (Figures 3 and 4). Decumbent tillers were also noted among the harvest plants processed at Succor Creek, but were infrequent, and their contribution to cheatgrass grazing avoidance in this study is uncertain. Possibly, decumbent growth played a role earlier in the season, after which point tillers developed more vertically and were consequently not counted at harvest. More detailed surveys regarding proportions of decumbent tillers done throughout the season in future studies would be useful in addressing this question.

Some of the surviving plants and flowering tillers might also be explained by tiller development following defoliation, though only one or two weeks had passed in the interim. At the end of the season, there were more tillers per plant in the SB1 clippings than in the control at Succor Creek. This result suggests that clipping cheatgrass low to the ground and earlier in the season may stimulate production of new tillers or elongation of existing tillers in cheatgrass following removal of the primary culm and before moisture becomes limiting—evidence that cheatgrass has traits of a grazing tolerant plant. The data for SB1 and SB2 treatments at Lincoln Bench suggest a similar pattern. The ability of cheatgrass to recover through tiller development was also observed in the study by Finnerty and Klingman (1962), where a few plants survived to develop tillers when plants were mown one week after the inflorescences had emerged. Thus, the variability in cheatgrass development and growth that could enable some plants to avoid defoliation, along with its capacity for grazing tolerance in early and possibly even mid-season clippings, supports the use of continuous or repeated grazing to capture all cheatgrass cohorts and regrowth.

Livestock Use and Management

Clipping cannot completely simulate grazing by animals. In a study of the effect of horse and sheep grazing on forage plants in the Himalayas, regrowth was better in clipped grasses than in grazed grasses (Negi et al. 1993), while other studies have found an increase in photosynthetic rates in grazed plants versus mown plants (Wallace 1990). Some of the differences in plant response following the different types of defoliation may occur since clipping or mowing cannot account for the effects of trampling, nutrient recycling, diet selectivity, or the grazing method of the animal. Thus, results of this study should only be considered as a guide for when defoliation might be most effective. We recommend that further studies of seed production be carried out using sheep and cattle as the defoliating agents.

All clipping treatments except the tall boot treatment contained enough biomass to support manageable numbers of sheep or cattle. This result supports the potential for a grazing management strategy to play a dual role in both controlling cheatgrass and providing forage for livestock. However, directing livestock to graze 100% of the cheatgrass plants in a given area may be difficult when confronted with their foraging behavior. Livestock tend to be energy maximizers and will therefore feed optimally, selecting the most nutritious and easily accessible forage (Stuth 1991). Considering this, livestock should be maintained in a fenced area to compel animals to graze all plants, including those less profitable to the animal. However, even then an animal might refrain from grazing the available forage if it is obtained at too great a cost versus the benefit gained (Coleman et al. 1989). This possibility is of concern when the objective of grazing is for cheatgrass control, particularly for removal of the smaller, single-seeded plants that were often observed in this study. Another potential obstacle to using livestock may be created by the presence of unpalatable secondary weeds. Curveseed butterwort (*Ceratocephala testiculata*), whose sharply pointed achenes become very hard upon maturity and could potentially cause injury to livestock, was very abundant at Succor Creek. Grazing cheatgrass low to the ground may not be possible for livestock under such conditions.

Conclusion

In two cheatgrass-dominated sites in the sagebrush-steppe ecosystem, intensive and repeated defoliation treatments conducted during initial inflorescence development clearly caused significant mortality to cheatgrass plants, reduction in plant reproductive ability, and reduction in the amount of cheatgrass seed entering the seed bank. However, these treatments were not able to completely prevent seed production, possibly due to the ability of cheatgrass to tolerate and avoid defoliation. If a similar grazing treatment with livestock has a similar effect, it may not produce the desired control over cheatgrass seed production that would be necessary to prepare seedbeds for native plant reseeding projects. However, increasing the defoliation intensity or using an integrated weed management approach with grazing in conjunction with other control methods such as herbicide application or burning (Mosley 1996; Whitson and Koch 1998) may achieve more complete control. Further studies considering these options, using animals as the defoliating agents, and establishing the necessary level of control should help clarify the practicality and effectiveness of using grazing as a step in the process of restoring native sagebrush steppe to the region.

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Appendix

Appendix A
Maps and Photographs

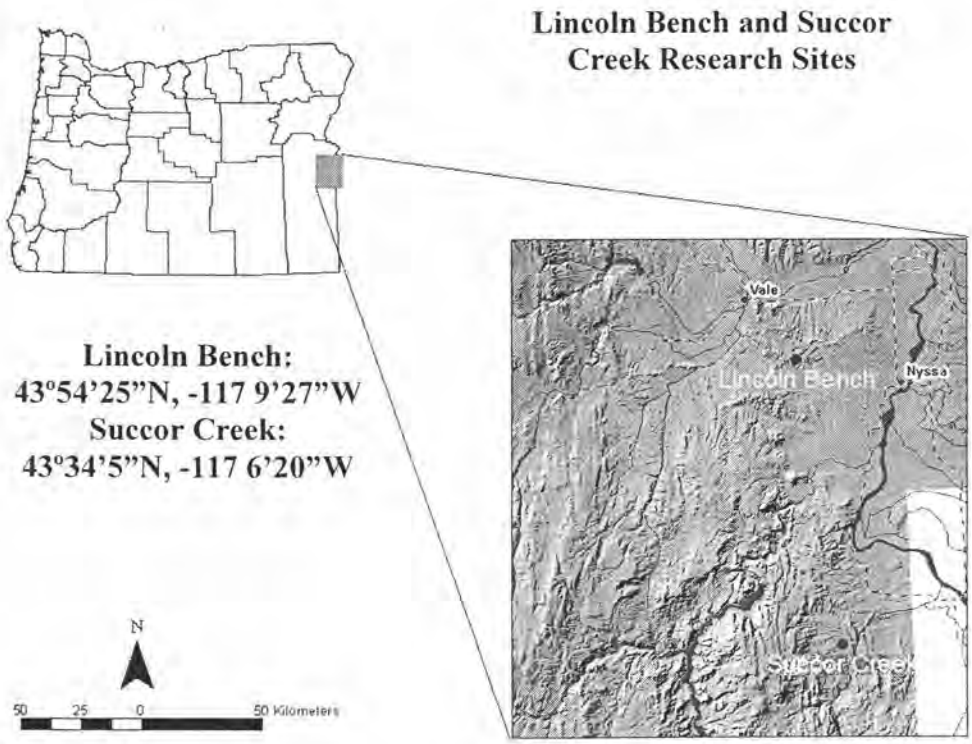

Figure 1. Map of Succor Creek and Lincoln Bench Research Sites.

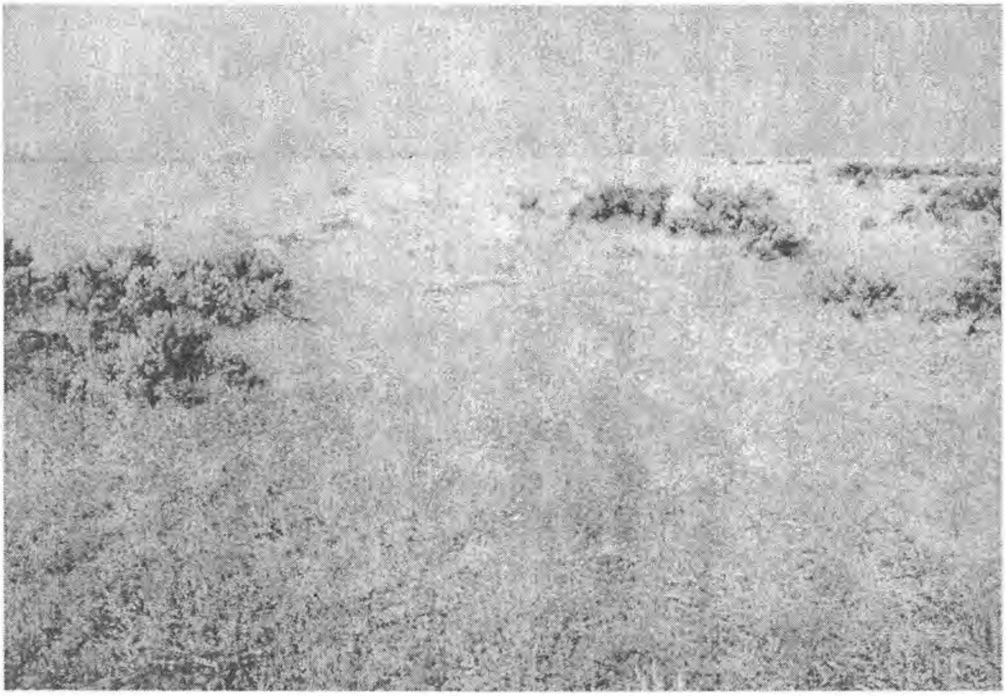

Figure 2A. Photograph of Lincoln Bench, August 2002.

Figure 2B. Photograph of Succor Creek, August 2002

Appendix B
Soil Descriptions

Succor Creek Experimental Site

The Succor Creek site is located on a toe-slope with approximately a 5% slope. Elevation is approximately 824 m. Dominant vegetation consists of cheatgrass (*Bromus tectorum* L.), annual wheatgrass (*Eremopyrum triticeum* (Gaertn.) Nevski), curveseed butterwort (*Ranunculus testiculatus* (Crantz) Bess.), bulbous bluegrass (*Poa bulbosa* L.), and redstem stork's bill (*Erodium cicutarium* (L.) L'Hér. Ex Ait.). Where annual wheatgrass occurs, soils seem to be effervescent at the surface. Average annual precipitation is estimated at 24.9cm.

Representative profile of Succor Creek experimental site at 43°34'5"N, -117°6'20"W, Malheur County, Oregon:

A1—0-23 cm, brown (10YR 5/3) silty clay loam, brown (10YR 4/3) moist; weak, coarse granular structure; slightly sticky and very plastic; common very fine roots; common very fine dendritic tubular pores; smooth boundary.

B1—23-50 cm, yellow brown (10YR 5/4) silty clay, dark yellow brown (10YR 4/4) moist; moderate very coarse granular structure; slightly sticky and very plastic; very few very fine roots; very few very fine dendritic tubular pores; strongly effervescent; smooth boundary.

B2—50-*64 cm, light yellow brown (10YR 6/4) silty clay loam, dark yellow brown (10YR 4/4) moist; moderate very coarse granular structure; slightly sticky and very plastic; few very fine roots; few very fine dendritic tubular pores; strongly effervescent; smooth boundary.

Lincoln Bench Experimental Site

The Lincoln Bench site is located on a hillside with approximately a 14% slope. Elevation is approximately 927 m. Dominant vegetation consists of cheatgrass (*Bromus tectorum* L.), bulbous bluegrass (*Poa bulbosa* L.), and redstem stork's bill (*Erodium cicutarium* (L.) L'Hér. Ex Ait.). Average annual precipitation is estimated at 28.5 cm.

Representative profile of Lincoln Bench experimental site at 43°54'25"N, -117°9'27"W, Malheur County, Oregon:

A1—0-11cm, brown (10YR 5/3) silty clay loam, dark brown (10YR 3/3) moist; structureless very fine granular, non-sticky and slightly plastic, with many very fine roots; many very fine dendritic tubular pores; smooth boundary.

AB—11-24 cm, brown (10YR 4/3) silty clay, dark brown (10YR 3/3) moist; moderate medium subangular blocky structure, slightly sticky and moderately plastic; many very fine roots; many very fine dendritic tubular pores; smooth boundary.

B1—24-44 cm, yellow brown (10YR 4/4) silty clay, dark yellowish brown (10YR 3/4) moist; moderate coarse subangular blocky structure; moderately sticky and moderately plastic; many very fine roots; many very fine dendritic tubular pores; smooth boundary.

B2—*44 cm, light yellow brown (10YR 6/4) silty clay, dark yellow brown (10YR 4/4) moist; very hard massive structure; moderately sticky and moderately plastic; moderately few very fine roots; common very fine dendritic tubular pores; smooth boundary.

*Soils were not analyzed below this depth.

Appendix C.
Residual and Box Plots

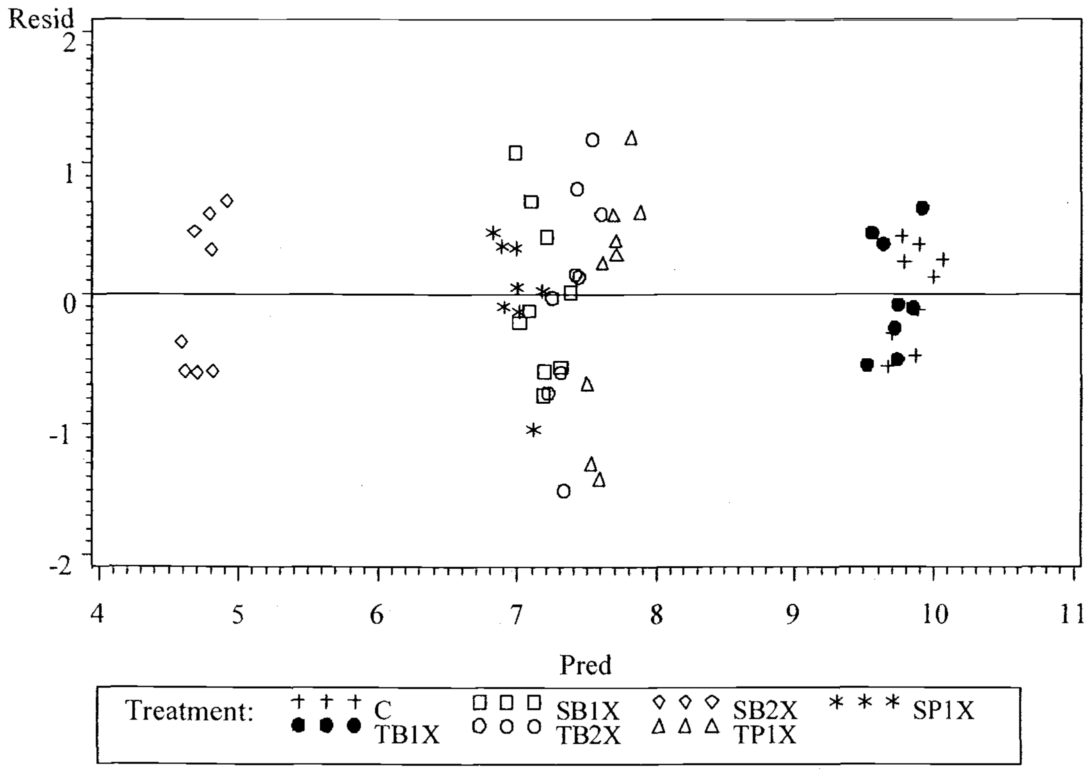

Figure 1A. Lincoln Bench residual plot of seed production (log seeds/m^2)

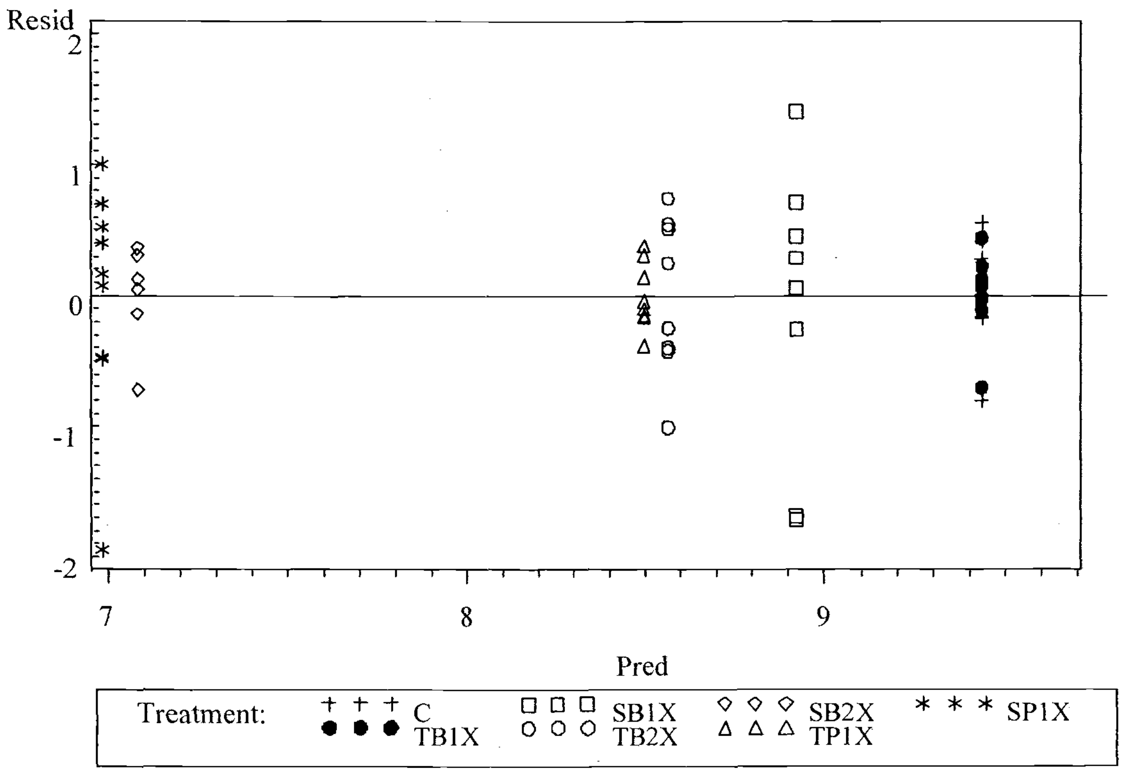

Figure 1B. Succor Creek residual plot of seed production (log seeds/m^2)

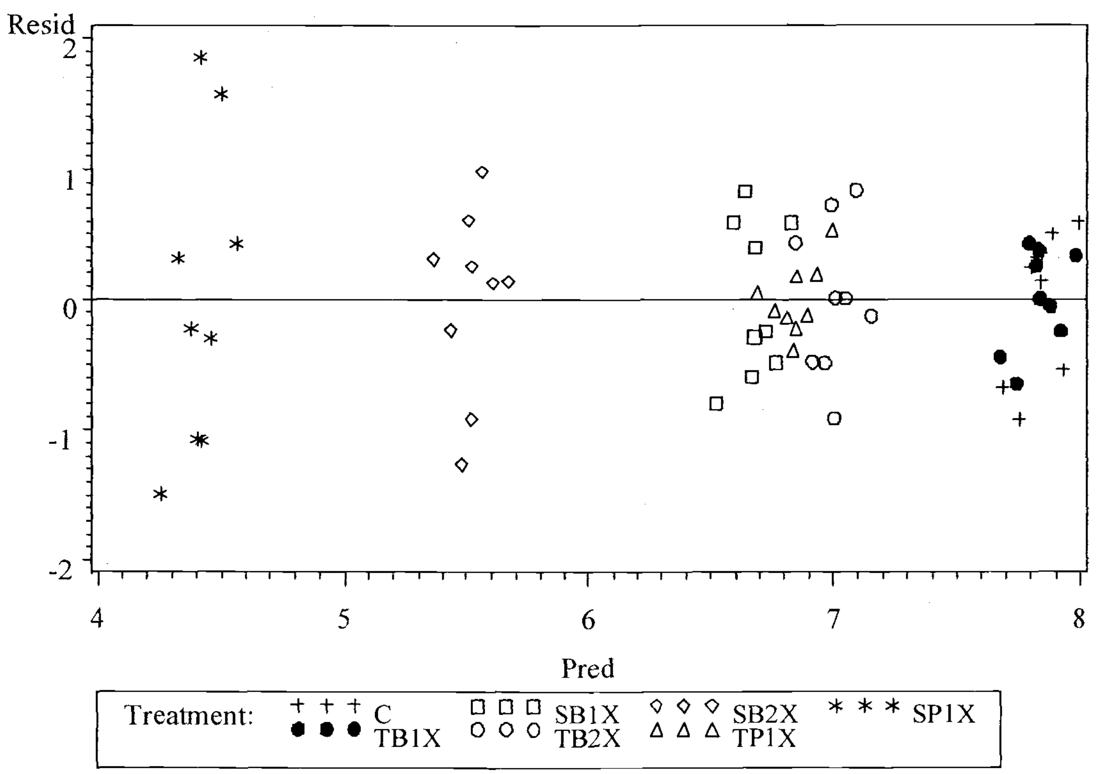

Figure 1C. Lincoln Bench residual plot of final density (log plants/m^2)

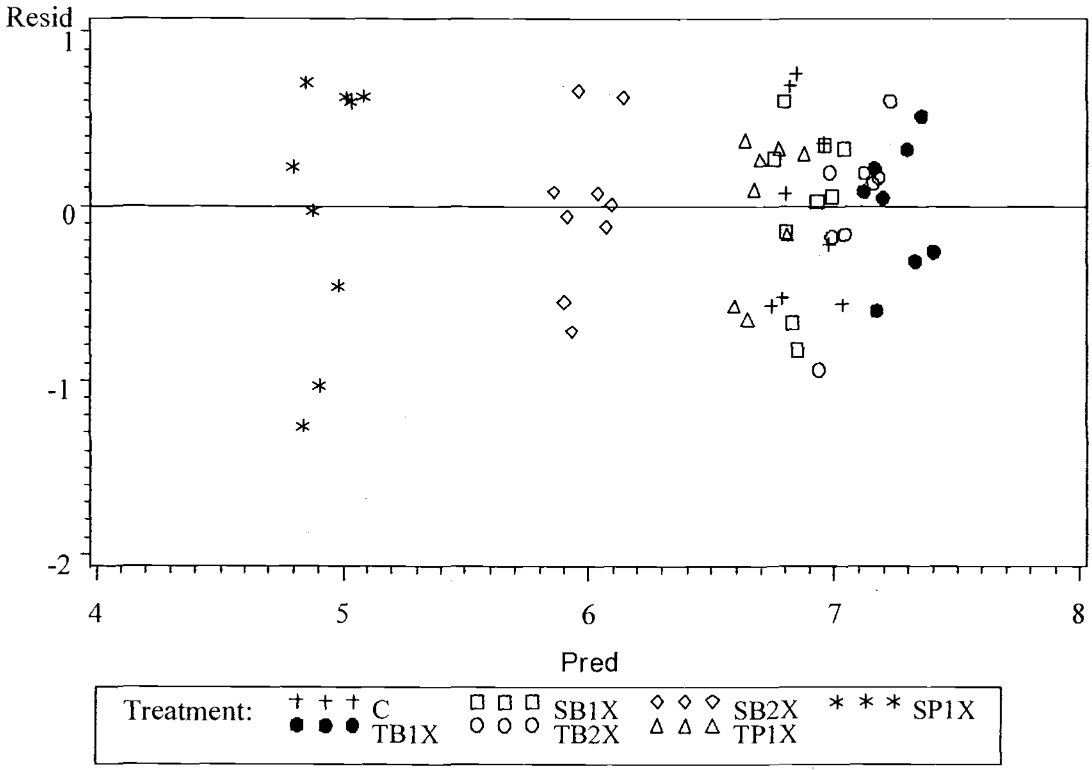

Figure 1D. Succor Creek residual plot of final density (log plants/m^2)

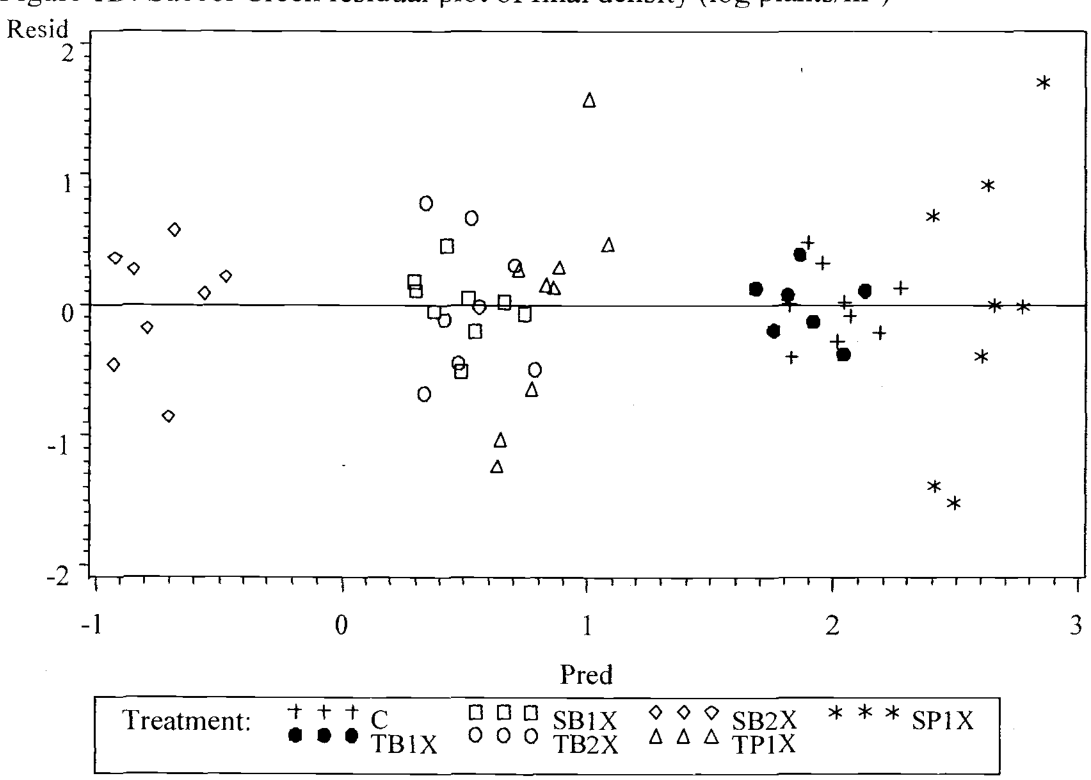

Figure 1E. Lincoln Bench residual plot of plant seed production (log seeds/plant)

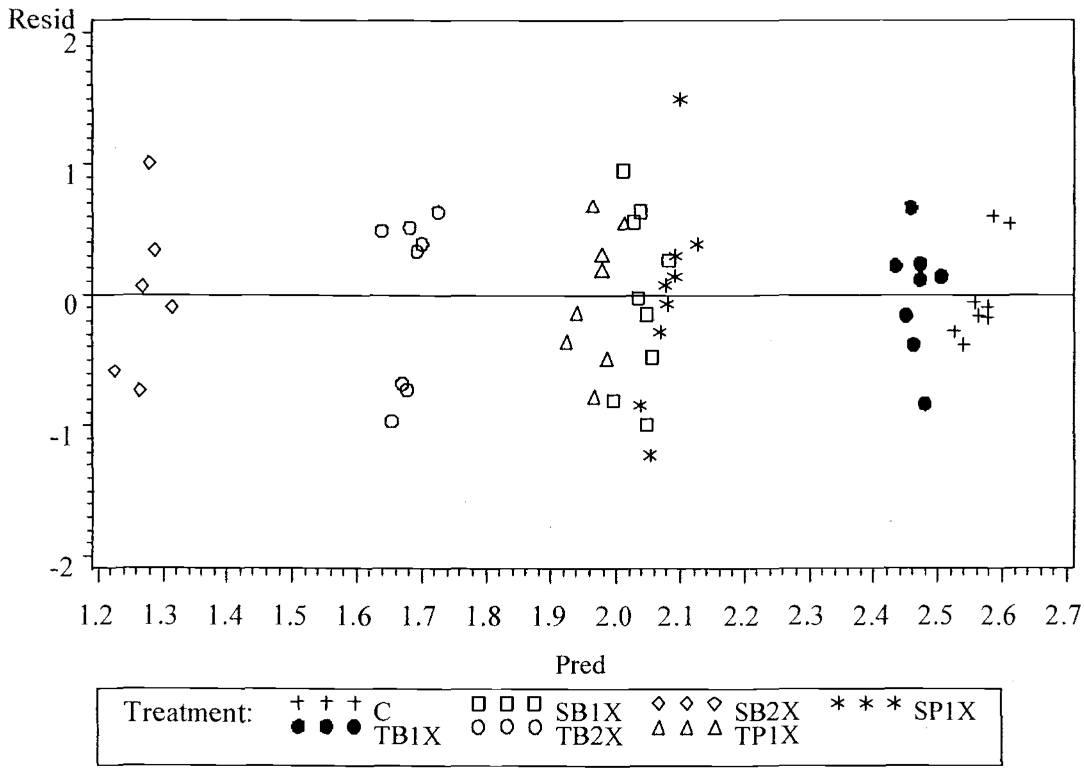

Figure 1F. Succor Creek residual plot of plant seed production (log seeds/plant).

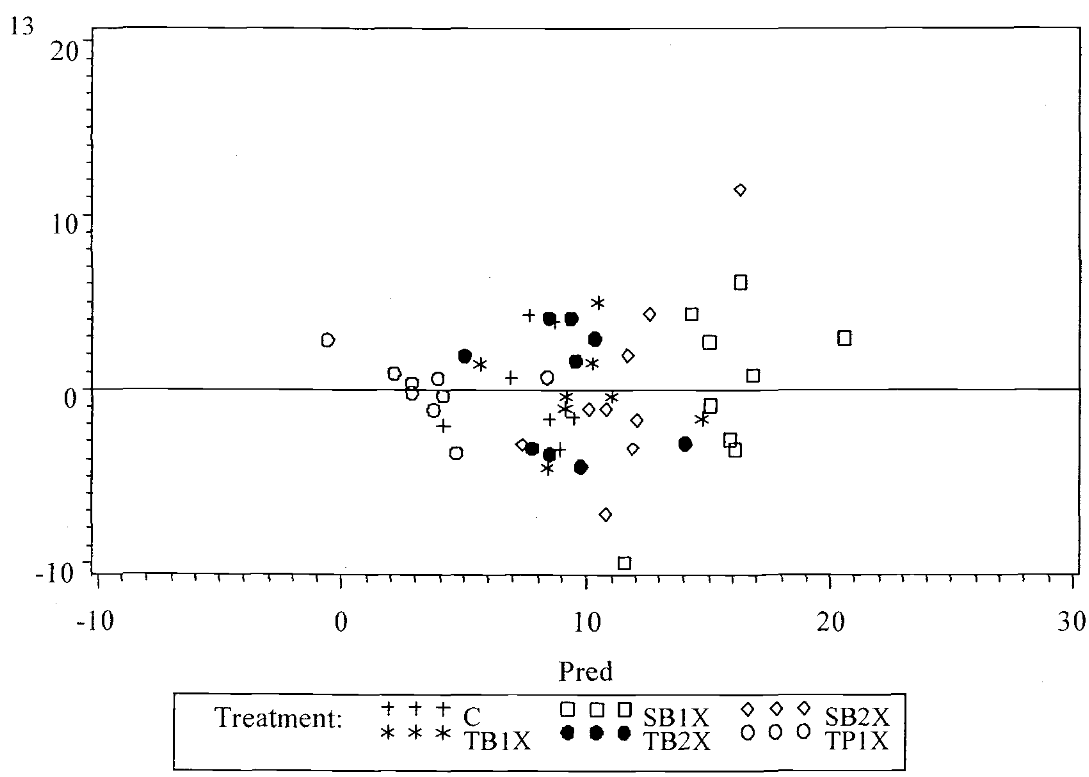

Figure 1G. Succor Creek residual plot of plant stem production (% plants with greater than 1 flowering stem).

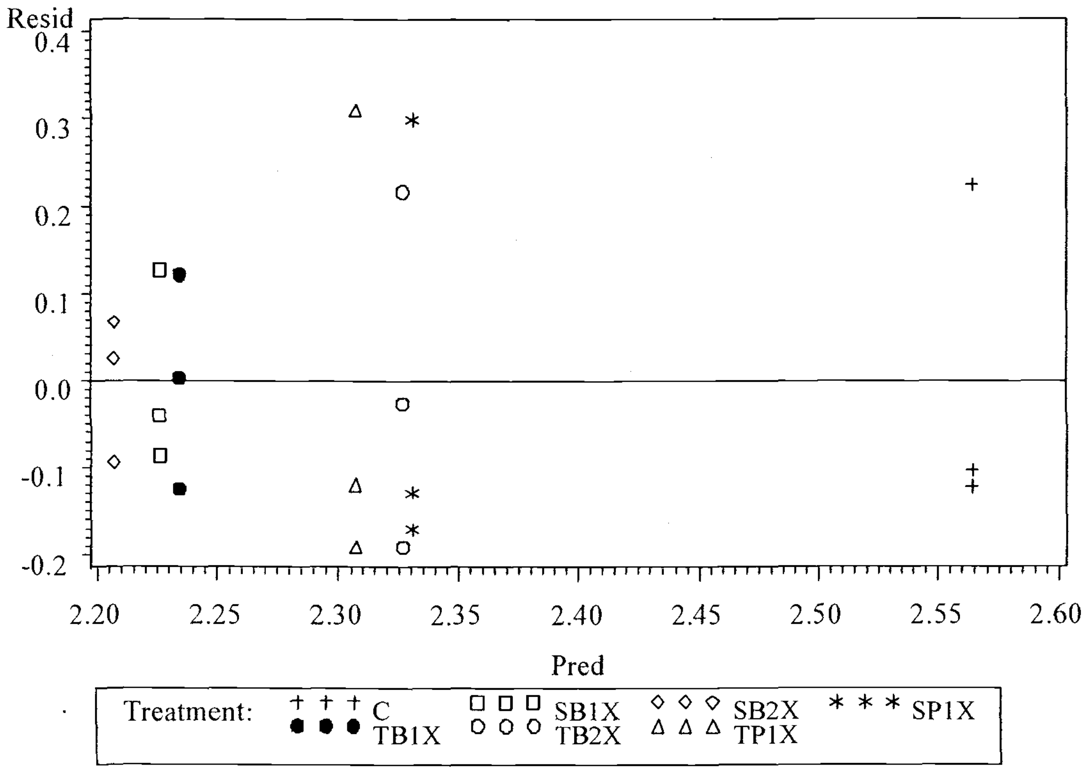

Figure 1H. Lincoln Bench residual plot of seasonal volumetric soil moisture (log %).

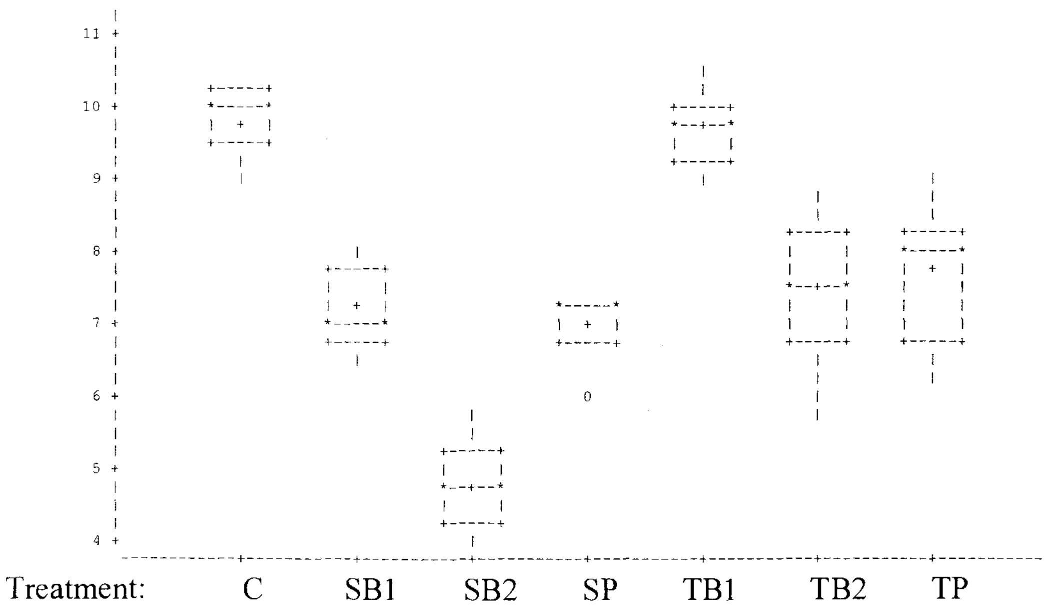

Figure 2A. Lincoln Bench box plots of seed production (log seeds/m^2).

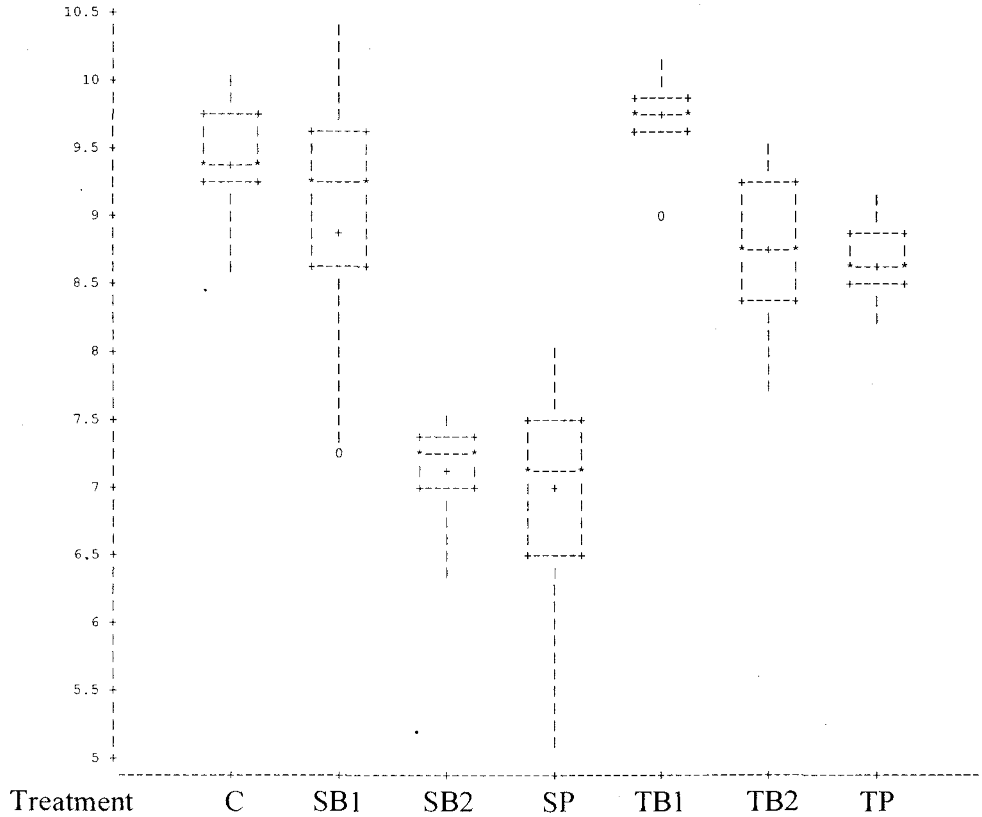

Figure 2B. Succor Creek residual plot of seed production (log seeds/m2).

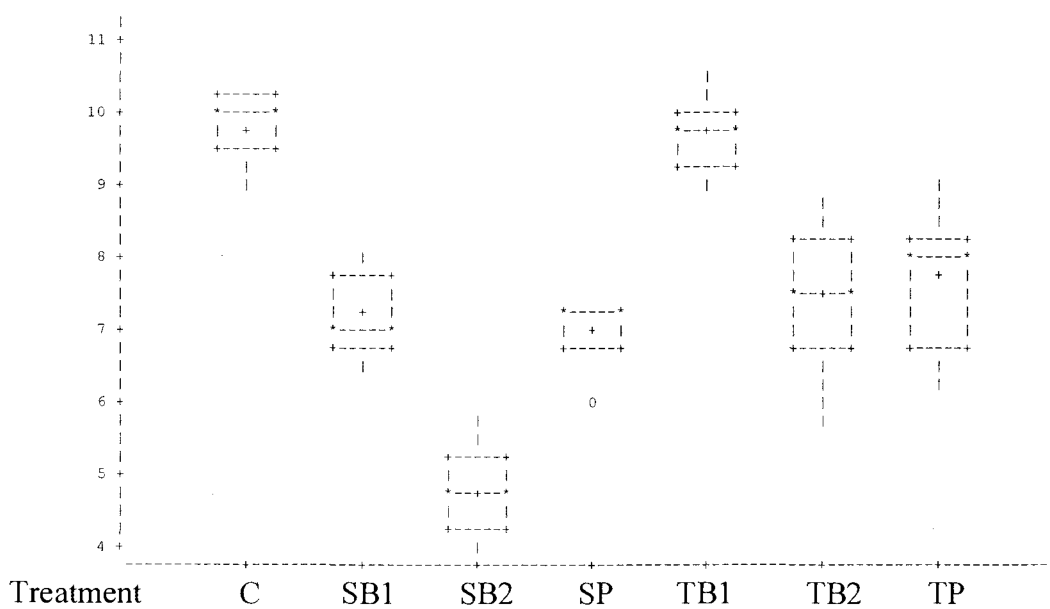

Figure 2C. Lincoln Bench box plot of final density (log plants/m^2).

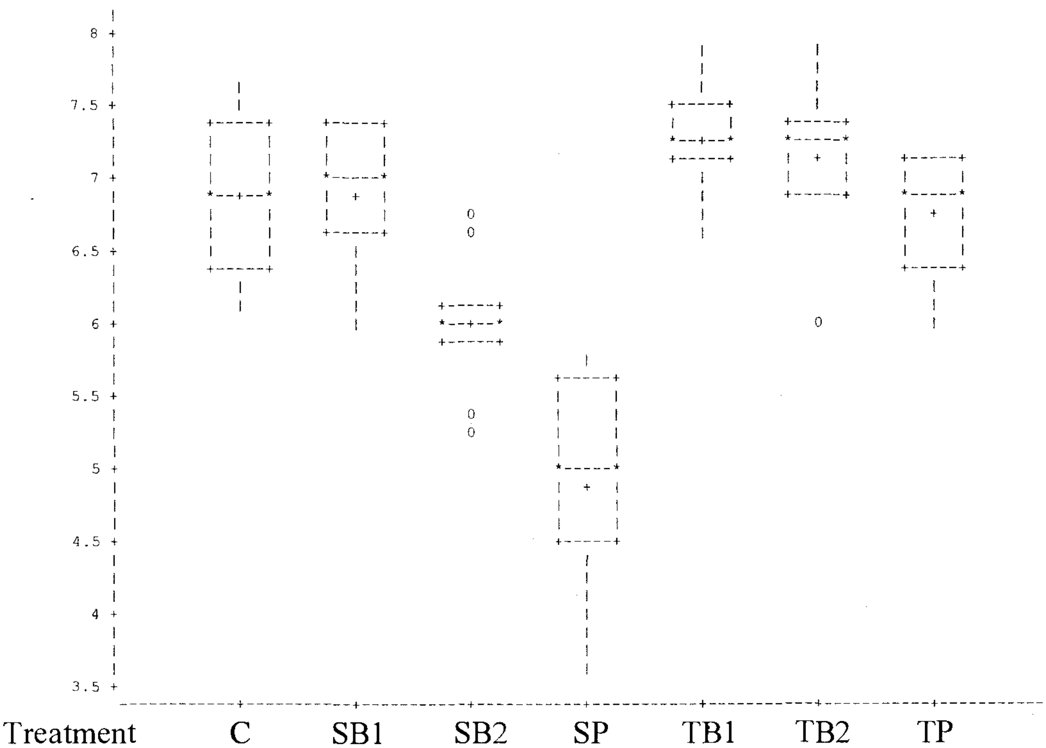

Figure 2D. Succor Creek box plots of final density (log plants/m^2).

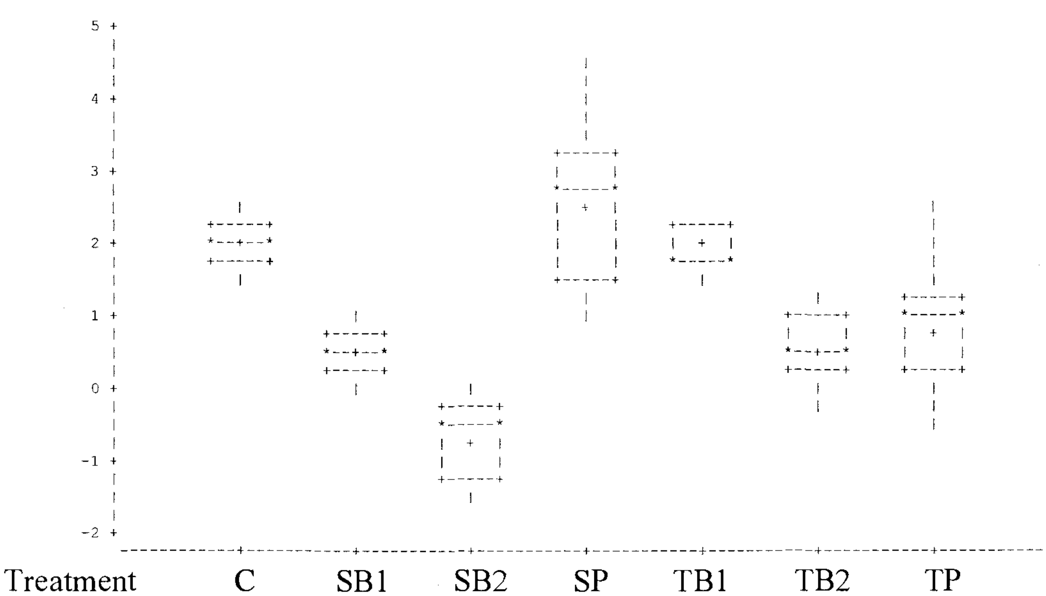

Figure 2E. Lincoln Bench box plot of final plant seed production (log seeds/plant).

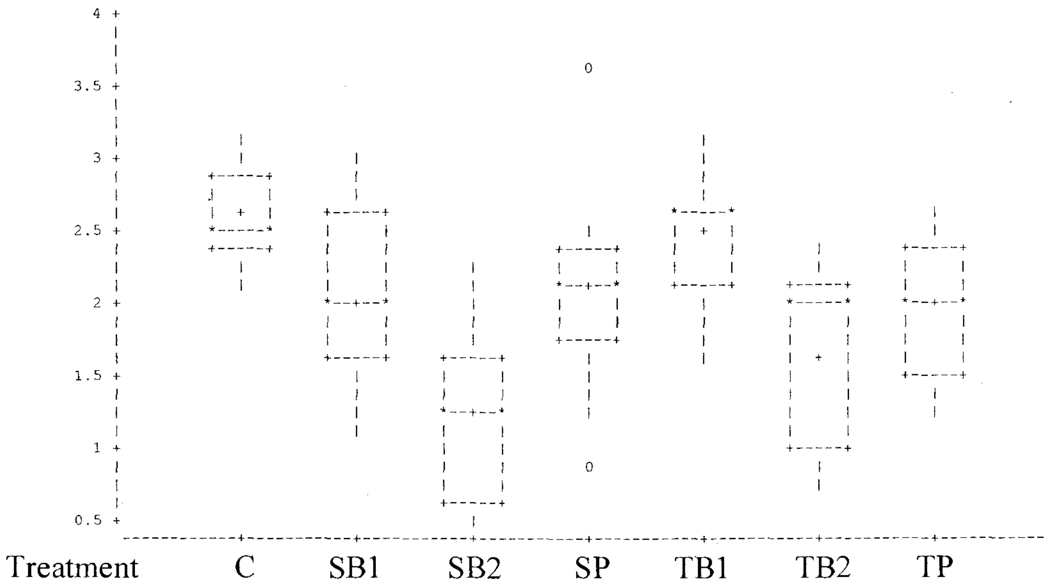

Figure 2F. Succor Creek box plot of final plant seed production (log seeds/plant).

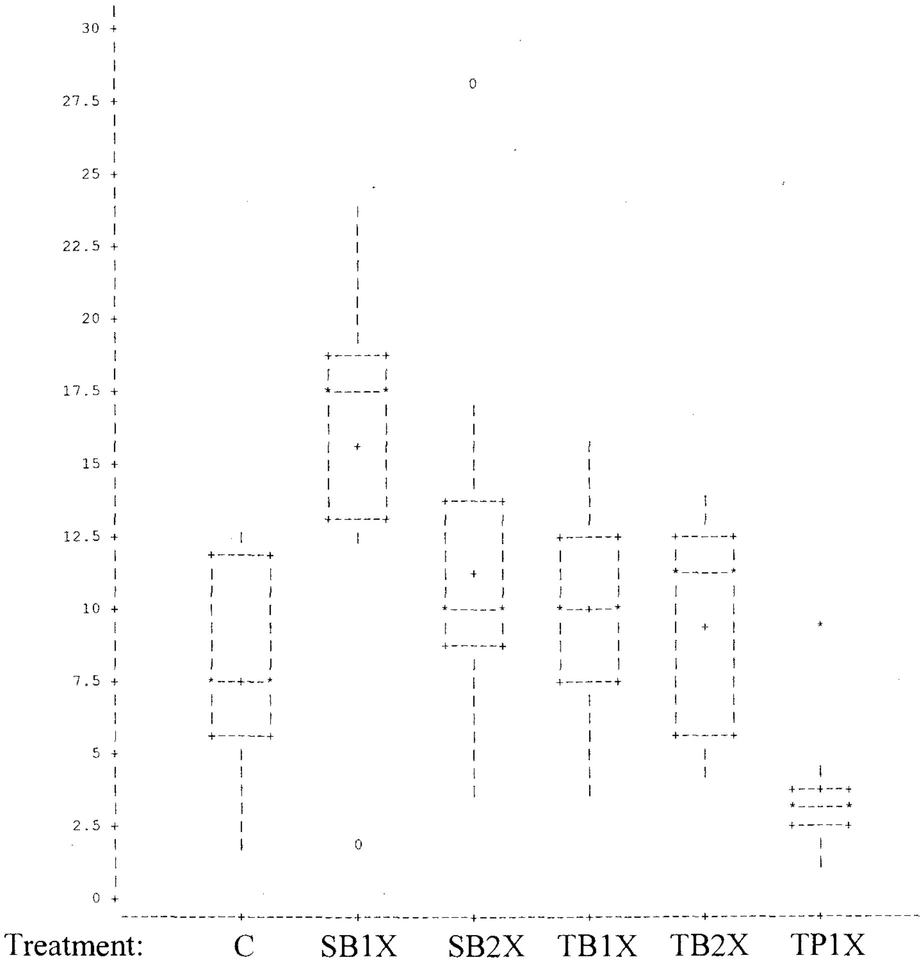

Figure 2G. Succor Creek box plot of final plant stem production (#plants with greater than 1 flowering stem).

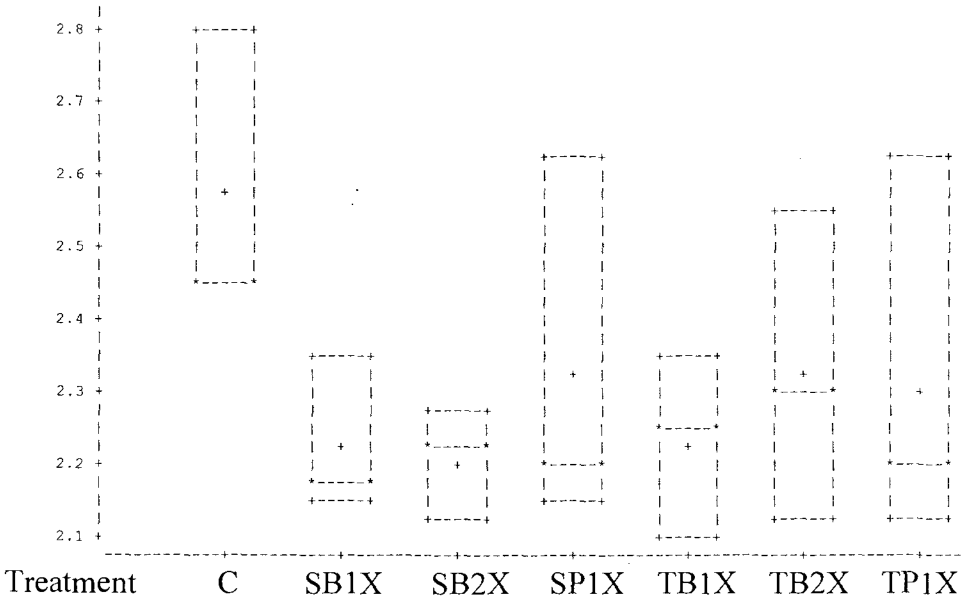

Figure 2H. Lincoln Bench box plot of seasonal volumetric soil moisture (log %).