2014-12-01

# Cheatgrass Die-Off Phenomena: What are the Short and Long Term Recovery Factors of Bromus tectorum Stand Failure?

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*Bromus tectorum* Stand Failure?


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A thesis submitted to the faculty of
Brigham Young University
in partial fulfillment of the requirements for the degree of

Master of Science


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December 2014

ABSTRACT

Cheatgrass Die-Off Phenomena: What Are the
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Observations of *Bromus tectorum* L. (cheatgrass or downy brome) monocultures have shown that populations are susceptible to stand die-off or replacement failures. Die-offs, where the seed bank from the previous year fails to emerge, occurs in cheatgrass stands and it is unclear the trigger or cause. The fungus *Fusarium* has been identified in plant and seed samples from die-offs and may drive die-off activity through pathogenicity. Die-off recovery may take several years but cheatgrass populations eventually reestablish.

The purpose of our study was to determine whether *Fusarium* is a potential player in a die-off, and understand how die-offs recover after multiple years of stand failure. Our objectives were to determine: 1- litter and water effects on die-off activity; 2- if fungal pathogens, such as *Fusarium*, decrease the proportion of cheatgrass emergence in a die-off; and 3- whether direct or broadcast seeding, water, and litter treatments increase establishment in recovering die-offs.

Litter absent plots had significantly ($P < 0.0001$ and $P < 0.001$) more emergence at 49.2% and 41% compared to litter present plots 21.3% and 23.7%. The litter absent plots significantly ($P = 0.0003$ and $P = 0.001$) increased survival (82% and 52%) compared to litter present plots (70% and 41%). Direct planted versus broadcast seeding had significantly ($P < 0.0001$) more emergence, 36% to 11.9%.

The addition of *Fusarium* inoculum to field plots did not effectively replicate anticipated disease levels. The fungicide treatment did not have a significant influence at either site. The results from the study indicate that nothing inhibits cheatgrass from establishing following a persistent die-off disturbance. A unique window may be available for land managers to revegetate natives in invasive populations as large quantities of cheatgrass seeds fail to emerge during die-off events.

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Cheatgrass Die-Off Phenomena: What are the Short and Long Term

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**INTRODUCTION**

*Bromus tectorum* L. (cheatgrass or downy brome) is an invasive grass that is native to Eurasia. It inhabits millions of ha across the Great Basin and has increased fire frequency from 60-110 years to every 5 - 10 years (Pimentel et al. 2005, Knapp 1996, Whisenant 1990). Cheatgrass is a selfing, winter annual grass that inhabits sagebrush steppe communities whose elevation is less than 2200m (Leger et al. 2009). It is highly competitive, difficult to eradicate, and colonizes shrub steppe communities after massive disturbance from sagebrush removal and livestock grazing (Yensen 1981, Mack 1981). Indigenous plant species struggle to establish in areas infested with cheatgrass because of the greatly increased fire frequency, and the copious quantities of seeds produced each year. Seed bank densities range from 10,000 to 30,000 seeds m$^{-2}$, which generate more dried plant material for fire and eventually creating a monoculture of cheatgrass (Beckstead et al. 2010, Meyer et al. 2007).

Invasive species damage ecosystem integrity and are responsible for reduced agricultural yield, native plant and animal declines, destruction of the fragile balance of habitats, and damage to US investments such as forestry. Invasive species cost the US economy $120 billion/year (Pimentel et al. 2005). This number is significantly underestimated when considering the cost of losses in biodiversity, ecosystem services, and aesthetics. Cheatgrass proliferation and establishment pose a continuing threat to the ecology of the Great Basin. Cheatgrass invasion is one of, if not, the most prolific example of exotic plant invasion in modern North America.

Cheatgrass has a high level of phenotypic plasticity and one plant m$^{-2}$ can produce as many seeds as 10,000 plants m$^{-2}$ (Young et al. 1969). These characteristics are important as desert plant communities have irregular, limited seed production, complex dormancies, and most species do not rely on seed banks. Cheatgrass has the potential to outcompete natives at the seed

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production and establishment level. The high annual production of seeds and the persistent seedbanks of cheatgrass allow it to dominate almost any community where it establishes.

Anthropogenic forces such as grazing pressure, desert plant and tree ecological modifications, and accidental introduction of species has helped propel cheatgrass to become a persistent problem. Grazing animals function in the long distance dispersal of cheatgrass by feeding on it as it comprises the bulk of forage on many rangelands. Cheatgrass was so favored for grazing that it was once deliberately seeded into new areas. Even prescribed fires and removal of sagebrush were common to supply greater forage for grazing animals in the Great Basin (Yensen 1981). During the 19th century, cheatgrass seeds were brought over as a grain contaminant and at the same time large scale domestic grazing took effect and livestock helped disperse cheatgrass seed throughout degraded rangeland. Overgrazing of cheatgrass during a dry season on ranges can lead to increased ecological degradation through excess soil erosion and loss of site potential (Young and Allen 1997).

Fire is the main factor in the persistence and survival of cheatgrass (Knapp 1996). Before the introduction of cheatgrass by European settlers, fires burned through xeric sagebrush-bunchgrass communities every 60-110 years (Knapp 1996). Fires were so infrequent in these communities because there was not enough fuel to keep a fire going. Cheatgrass is an excellent source of fuel because it drops seed in the late spring, and dries out. In addition, the arid nature of deserts does not decompose cheatgrass litter fast enough and the litter can accumulate over the years. The remaining dense dry litter acts as an excellent source of fuel for fires. Fire frequency, which can occur as often as every 3-5 years, results in the establishment of thick monocultures across the Great Basin because native shrubs and grasses do not establish as quickly.

The frequent and intense fire regimes have reduced the species richness across desert flora as cheatgrass continues to dominate. Cheatgrass is an early successional species and is able to establish before native perennials. The post fire resource for plant growth is freely utilized by cheatgrass. Cheatgrass litter accumulation has propelled fire ranges into areas that once did not typically have natural fire disturbance. These newly degraded areas are susceptible to cheatgrass invasion and establishment as disturbance increases the mineralization of nitrogen; cheatgrass thrives on nitrogen enrichment (Harris 1967). Millions of dollars are spent annually on seeding burned areas caused by the presence of cheatgrass and on funding research programs to control its spread and to suppress intense fires caused by its presence. It is important that as cheatgrass continues to invade the Great Basin, we understand the effects and how to reduce fire intensity and frequency.

Cheatgrass reacts quickly to the availability of light and nutrients and is the most advantageous in establishment in post Great Basin fire disturbances. It has been shown that the dispersal distance of cheatgrass seeds was higher in burned over that of unburned sites (Monty et al. 2013). Wind is the primary force that blows cheatgrass seeds into new plant communities after disturbance. Unobstructed wind increases the dispersal distance. It has been revealed that fire can stimulate the destruction of mature plant communities but can also enhance the dispersal distance of cheatgrass seed, therefore increasing invasion (Monty et al. 2013). Cheatgrass is rapidly altering Great Basin plant communities and increasing its range, it is critical that practical control methods are implemented and utilized.

Cheatgrass monoculture observations have revealed that populations are susceptible to stand die-off or replacement failures (Piemesel 1951). Die-offs, where the seed bank from the previous year fails to emerge, may occur in cheatgrass stands but it is unclear the trigger or

cause. Areas that supported hundreds of cheatgrass plants per square meter lack even a single plant (Baughman and Meyer 2013). Disturbed areas where seeds were able to persist in the soil for two or three years may recover in the short term, but some areas have been observed where cheatgrass did not recover. In these areas where recovery is long term, it appears that cheatgrass seeds are unable to establish in these areas following a die-off disturbance, even with an apparently viable seed bank that can persist for a few years. These long-term die-offs are now bare ground and lack plant stands. This study seeks to understand the short-term recovery of die-offs; as well as, the long term recovery, those die-offs that persist for many years and eventually become bare ground.

Plant and seed samples collected from a die-off have confirmed the presence of multiple fungal pathogens (Meyer et al. 2014). *Fusarium* species were the most isolated fungus from cheatgrass seeds and seedlings in die-off soils and found to cause cheatgrass seed death (Meyer et al. 2014). *Fusarium* species are also known pathogens and can reduce yields in wheat crops through crown rot disease (Moya-Elizondo 2013). Some *Fusarium* species are considered "unspecialized" pathogens because they can attack any plant (corn, wheat, and some broadleaf crops) tissue if conditions at the tissue surface are favorable (Paulitz et al. 2002). In vitro studies have shown that cheatgrass seed pathogenicity by *Fusarium* infects and kills non-dormant seeds (Beckstead et al. 2007).

*Fusarium* may play a role in driving die-offs but for recovery to take place we assume pathogen populations must decrease. Die-off recovery may take several years but are not a permanent disturbance as cheatgrass populations eventually reestablish. Recovery in the first or second year after a die-off event is dependent on the persistent seed banks that hold secondary dormant seeds that will survive and establish (Baughman 2013). It has been observed that die-

offs can reestablish cheatgrass stands in the coming years through secondary dormant seeds in the seed bank and restore monocultures to full force (Baughman 2013). However, some die-offs fail to recover the following year, even though these areas are typically surrounded by cheatgrass monocultures. Prolonged die-offs are characterized by bare soil that becomes populated with summer annual weeds such as Russian thistle, bur buttercup, and annual kochia. These old die-off areas are typically surrounded by cheatgrass monocultures, but the seed bank is depleted so it is assumed that seeds must be dispersed into the area for reestablishment to happen.

Prolonged bare ground die-offs need wind-blown seed to reestablish, however, cheatgrass prefers to invade areas that already have some level of establishment by other plants. The presence of litter from the other plants may enhance the establishment of cheatgrass in old die-offs. Little is known about the components and factors of die-off activity and how die-offs recover after multiple years of stand failure in both the short and long term, therefore the purpose of our study it to fulfill broad multiple working hypotheses. Understanding old die-off characteristics from seed and litter manipulations could reveal why die-offs even occur and how land managers could harness post die-off activity, to inhibit the recovery of cheatgrass, and aid in the establishment of native shrubs and grasses.

**Short-Term Recovery.** [1] If there is a residual effect of a soilborne pathogen that caused a previous-year die-off, then cheatgrass will have increased emergence, survival, biomass, and plant count of cheatgrass in areas that did not experience a die-off relative to areas that experienced previous-year die-off. Die-offs always leave behind thick grey matted litter after disturbance and there could be a link between disease and litter. [2] If soilborne pathogens are more active under high-litter conditions, then removing litter should reduce disease and increase emergence, survival, biomass, and plant count. [3] If soilborne pathogens are more active at low

water potentials that do not permit seed germination, then adding a small amount of water (ca. 1.2 cm) to the plots following planting will stimulate pathogen activity and permit infection under water stress, thereby decreasing emergence and survival. [4] If emergence failure and seedling death are caused by soilborne pathogens, then increasing the inoculum load of a known pathogen, such as *Fusarium*, will decrease emergence and survival. [5] The application of a fungicide could negatively impact soilborne pathogens and increase emergence and survival of cheatgrass.

**Long-Term Recovery.** [1] If a lack of seed limits recruitment onto old die-offs because the in-situ seed bank has been depleted, then seeds either are not dispersing well or they are not being retained on the smooth surface of bare soil. Therefore a direct and broadcast cheatgrass seeding treatment will test retention and increase establishment success. [2] Further, if water is limiting to establishment on bare soil with little organic matter, then application of adequate water (2.5cm) might be enough to encourage cheatgrass seedling emergence. [3] A field application of sterile autoclaved cheatgrass litter to a bare ground plot might improve seed retention and possibly also establishment.

## MATERIALS AND METHODS

**Short-Term Recovery.** A site for the 2012-2013 season was selected in the valley of Dun Glen, Nevada (40°41.25′N 117°57.22′W, elevation 1382m, average annual precipitation 175mm) and the following season 2013-2014 near the White Rocks road, Utah (40°19.68′N 112°46.68′W, elevation 1446 m, average annual precipitation 199 mm). A fence surrounded each study location to eliminate grazing disturbance.

Treatments for Dun Glen and White Rocks included litter present (L+) or absent (L-), control (C), inoculum (I), fungicide (F), die-off (DO), cheatgrass monoculture (CM), and water

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present (W+) or absent (W-). The experimental layout for Dun Glen was a split plot design with 10 blocks. In addition, the experimental layout for White Rocks was a split split plot design. The paired treatment for the Dun Glen site was DO and CM, with all other treatments such as C, I, F, L, and W as completely randomized within the blocks. The paired treatments for White Rocks were DO and CM, which were divided into 3 sub-treatments C, I, and F, that were further subdivided into 4 sub-sub-treatments L+, L-, W+, and W- (Tables 1-4). A total of 24 combinations were evaluated for cheatgrass emergence and mortality. Litter absent treatments had all above ground plant litter and biomass removed from the plot while leaving the soil intact. Litter present treatments did not have litter removed and were kept in their natural state. The Dun Glen study was installed in October 2012 and the White Rocks study was installed on September 20, 2013.

Recent die-offs were identified by the lack of cheatgrass production and presence of the previous year's thick grey litter. Typically these areas had less than 5 cheatgrass plants in a $0.1m^2$ plot. The selected areas also hosted summer annuals such as Russian thistle and mustard, which were removed from the study area prior to treatment installation. Cheatgrass monoculture areas had more than 5 cheatgrass plants in a $0.1m^2$ plot, did not have extensive cheatgrass litter, and had healthy stands.

We followed the standard protocol 'Media for the Preparation of Natural Inocula' to craft 2.4kg of oat grain chaff medium of the *Fusarium* species for soil application (Summerell et al. 2001). Cereal chaff and grain were mixed to 5:1 ratio. We added 500mL of chaff grain mixture to 2L beaker and add 1L of water. Phenolic compounds were leached by placing a beaker at 5°C overnight. We then drained mixture using cheesecloth and distributed chaff grain into Erlenmeyer flasks. The flasks were then sealed with cotton plugs and autoclaved for 15 minutes

on two successive days. Containers were inoculated with conidial suspension ($\geq 10^5$ cfu/ml) at the rate of 2ml of the fungal suspension per 250 ml chaff grain mixture. The inoculated material was incubated at 25°C for 14 days. Cultures were shaken daily for the first 3-4 days to encourage rapid and uniform colonization. Once colonized, the chaff grain air-dried overnight at room temperature (20-25°C). When dry, the inoculum was crushed and passed through a 2mm sieve for addition to soil. In the field, the inoculum was applied to the plot at 30g and was spread evenly across the plot.

We applied 1.2 cm of water to the $0.1m^2$ plots. We set up two 5x10x30cm wood blocks alongside the right and left side of the plots. A galvanized wire cloth with dimensions of 35x35cm was placed on top of the wood blocks. A heavy duty gallon Ziploc bag was filled with 1174mL of water and placed over the galvanized wire cloth. Water was applied over a 20 to 30 min period by punching 4 holes in each corner of the water-filled plastic Ziploc bags suspended over the plots on wire frames. This allowed the water to infiltrate without running off. The plots were watered within an hour after the inoculum, litter treatments, and seeds had been planted.

Cheatgrass seed for all studies was hand collected from their respective sites before installation. We checked seed maturity and viability after we collected the seeds to make sure they were ready for experimental use. All collected seed was stored to dry-after-ripen at room temperature before being glued to toothpicks. Cleaning seeds required removal of the sterile florets from the base of the seed. The direct seeding method for this study involved gluing seeds to toothpicks with Titebond wood glue (Titebond, Columbus, OH) (Leger et al. 2009). The awn was pointed up with the palea facing outwards when glued to the toothpick. Toothpicks with attached seeds were inserted into the mineral soil until the body of the seed (i.e., the caryopsis with associated lemma and palea) was completely covered, leaving the awn tip and most of the

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toothpick above the soil surface. Toothpicks were arranged into a grid pattern 6.35cm apart in four rows of five seeds (n = 20 per plot). After seeds were glued to toothpicks, seeds for the fungicide treatment at Dun Glen were coated in Captan 50-WP fungicide (Micro Flo Company, Memphis, Tennessee) and left to dry for 24hrs.

Plots were evaluated multiple times to assess the status of each planted seed (Dun Glen: November 2013, March and May 2014 / White Rocks: November 2014, March and May 2014). Seedlings were marked by placing colored paperclips around both the new seedling and its attached toothpick (Leger et al. 2009). Each time plots were read, previously emerged seedlings were scored as dead or alive. Response variables analyzed included emerged seedlings/total planted seeds (seedling emergence) and seedlings surviving through spring/emerged seedlings (seedling survival).

Biomass of cheatgrass was collected in June 2013 (Dun Glen) and May 2014 (White Rocks). Biomass was collected to understand treatment effects on both experimental and non-experimental plants within the plot. All above ground biomass was removed from each plot after our last emergence data collection, when the cheatgrass was maturing. We were only concerned with cheatgrass and all other plant species were not included in the biomass collection. The collection was then placed in an oven chamber for two weeks at 65°C. Plant biomass was dried and weighed and recorded in grams/plot. We collected biomass to understand both experimental and non-experimental plant dynamics within the study.

Minimum modifications were made to the White Rocks site for the 2013-2014 portion of the study. The changes were: 1- toothpicks were planted into the soil in litter present plots; 2- all uninoculated plots received oat grain chaff at 30 g/plot; 3- Captan fungicide was not applied, instead a spray application of Maxim 4FS (Syngenta Crop Protection, Greensboro, North

Carolina) was applied on October 9, 2013 to fungicide plots (application rate of 12ml of Maxim4FS/2L of water to 13.9m$^2$ using a 1 gallon RL Flo-Master hand sprayer model 1401WM); and 4- die-off and cheatgrass plots were separated by 12m rather than 50m.

**Long-Term Recovery.** An area was identified within the White Rocks site that was an old unrecovered die-off for the 2013-2014 study. The design includes a randomized block design with experimental treatments that included litter present or absent, and supplemental watering present or absent, and direct vs. broadcast seeding, The design included 8 treatment combinations with 10 blocks for a total of 80 plots 0.10m$^2$ plots and was installed in the field October 2013. The 10 blocks were kept close together but locations were chosen to avoid areas of rodent and ant activity. Each block was installed within a bare soil area that completely lacked cheatgrass litter and was largely or completely devoid of cheatgrass plants, though summer dicot annuals were present at low to moderate densities.

Both seeding methods used the same cheatgrass seed collection as mentioned above and the direct seeding technique was the same described earlier. Broadcast seeding consisted of scattering 100 cleaned seeds across the 0.1m$^2$ plot.

Cheatgrass litter was collected from the Brigham Young University farm near Spanish Fork, Utah, chopped into small pieces to fit into field plots, and dry autoclaved for 45min. The litter present plots received 15g of autoclaved litter that was spread evenly across the plot. A 35x35cm garden mesh cloth was laid over the plot with garden staples in each corner to keep litter intact through the season. The watering treatment consisted of 2.5 cm applied using the previously described technique.

Our only response variable was plant number/plot. This was done by counting all established mature cheatgrass plants within each plot at the end of the season in both the direct

and broadcast seeding treatments. In the direct seeded plots, plants that were not attached to toothpicks (non-experimental) were recorded as natural recruitment or dispersal of cheatgrass into the plot. We collected plant number response variables in May 2014.

Statistical Analysis: Data from the seeding experiments at Dun Glen and White Rocks were analyzed using mixed model ANOVA with SAS Proc Mixed. Proportion variables were transformed using arcsine square root and biomass variables were log transformed to increase homogeneity of variance prior to analysis. Values in figures are means from 10 block replicates for each treatment with standard error. Figures 1A-D and 2A-D are connected with the short-term recovery study and the response variables include percent emergence, percent survival, biomass, and plant count. Figure 3A-C contains the long-term recovery study. The response variable plant count for both figures 3A and 3B are read on the left axis, whereas figure 3C with response variable percent emergence is read with the right axis.

**RESULTS**

**Short-Term Recovery.** Emergence was significantly ($P = 0.0166$) higher in die-off plots verses cheatgrass plots, 40.6% and 29.5% respectively, at Dun Glen (Figure 1A). However, at White Rocks die-off had more emergence than cheatgrass and was not different from each other, 33% and 31%, respectively ($P = 0.650$) (Figure 1A). Litter absent plots at Dun Glen and White Rocks had significantly ($P < 0.001$) more emergence at 49.2% and 41% compared to liter present plots 21.3% and 23.7% respectively (Figure 2A).

At Dun Glen and White Rocks, emerged seeds in die-off plots had slightly higher survival (79% and 50%) compared to intact cheatgrass plots, but it was not a significant effect (73% and 43%) ($P = 0.0846$ and $P = 0.4338$) (Figure 1B). Litter absent treatments at Dun Glen

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and White Rocks significantly (P = 0.0003 and P = 0.001) increased survival (82% and 52%) compared to litter present plots (70% and 41%) (Figure 2B).

Die-off areas had significantly (P < 0.0001) more plant biomass at Dun Glen than the cheatgrass monoculture, 15g vs. 7g/plot, respectively (Figure 1C). Results were opposite the following year at White Rocks, there was significantly more biomass in the cheatgrass plots (7.1 g/plot) compared to die-off plots (5.2 g/plot) (P < 0.0001) (Figure 1C). There were no significant differences in biomass between litter treatments at Dun Glen (P = 0.629) or White Rocks (P = 0.875) (Figure 2C).

Plant counts of experimental plus natural cheatgrass plants were not significantly different at P=0.0676 at Dun Glen (Figure 1D). The outcome was reversed the following year at White Rocks where there were significantly (P < 0.0001) fewer plants in the die-off treatment (33 plants/plot) compared to cheatgrass (150 plants/plot) (Figure 1D). This may reflect fewer seeds due to a lower density of seeds not being deposited back to the seed bank due to die-off disturbance.

There were no significant differences in plant count between litter absent and present plots at Dun Glen or White Rocks (Figure 2D). Plant count may be confounded by the possibility that removing litter may also remove in situ seeds, so that one would expect fewer plants in the litter absent plots because of seed limitation alone.

Water, inoculum, and fungicide treatments effects were not significant at either site. Across the whole experiment at Dun Glen fungicide, inoculum, and water emergences were 33%, 37%, 37% (P = 0.47, P = 0.65, P = 0.22). At the White Rocks site fungicide, inoculum, and water emergences were 23%, 26%, 26% (P = 0.16, P = 0.76, P = 0.82).

**Long-Term Recovery.** Natural recruitment of cheatgrass, which is the dispersal of cheatgrass seeds into the experiment, was 8.2 plants/plot for the whole experiment whereas the broadcast seeding treatments were significantly ($P = 0.046$) higher at 11.9 plants/plot (Figure 3A). Natural recruitment of cheatgrass into the experimental plots significantly affected plant count by increasing the number of plants from 5.6 in litter present plots to 10.8 in litter absent plots ($P = 0.04$) (Figure 3B). The use of direct planted compared to broadcast seeding treatments at White Rocks had significantly ($P < 0.0001$) increased emergence of cheatgrass, 36% to 11.9% respectively (Figure 3C). There were no effects on emergence from the addition of water. There were also no significant differences in litter present or absent on both direct seeded or broadcast treatments (data not shown).

## DISCUSSION

Results from the short-term die-off study suggest that leftover grey matted litter is deleterious to cheatgrass establishment as seeds are subject to unsuitable conditions resulting in mortality. It is still unclear why the presence of litter impeded cheatgrass establishment but pathogens could be implicated because studies have shown that litter facilitates disease at the soil-litter interface (Beckstead et al. 2012; Facelli et al. 1999). Our study was intended to solidify the pathogen interactions by using litter as a refugium for pathogenic fungi and generating microsite conditions that encourage disease. Then the fungicide would be added to reduce pathogen populations and inoculum was added to increase seed mortality by encouraging pathogenicity. However, our data showed no significant differences between fungicide and inoculum applications, which would have suggested an influence of pathogens on cheatgrass mortality, and the results neither prove nor disprove pathogen influence on the seeds (Figure 2A-D).

The varying seed placement for litter absent and litter present plots at Dun Glen support the suggestion that seeds are not able to establish if they do not make contact with the soil. The litter absent plots' seeds were placed 1cm into the soil whereas the litter present plots, seeds were placed 1cm above the soil and left in contact with the dense matted litter. Our purpose for varying seed placement between treatments was to simulate natural conditions where the seeds would fall into the litter and become suspended above the soil. We did not anticipate that seeds planted 1cm above the soil in the litter may go dormant during the growing season and, as a consequence, not be able to effectively germinate. We recognize that the litter effect on emergence could be due to experimental design and we infer results with caution from the first year of the study in Dun Glen. Differences in emergence at Dun Glen between litter removal and intact litter plots for planted seeds could have been an artifact of the shallow planting placement into litter, because, on a plot count basis, no such effect of litter removal could be detected. However, at White rocks we got a large negative effect of litter on emergence even when the planting depth artifact was removed, so it is plausible that even with a misfortunate planting depth, the trends are true for both sites where litter decreased emergence. It also remains possible that the litter increased disease mortality as it is unknown what limited cheatgrass emergence and survival.

Emergence and survival data from the die-off and cheatgrass treatments at Dun Glen suggests that cheatgrass establishes as well or better the year following a die-off event as it does in stands of full functioning cheatgrass monocultures, however, the White Rocks comparison was completely the opposite (Figure 1A, B, C). It is not clear whether die-off or cheatgrass monoculture areas present a more suitable opportunity for newly establishing cheatgrass and which ecological direction recovery will occur after a die-off disturbance.

It is intriguing that there were two mixed outcomes regarding activity of cheatgrass after a die-off but it appears to be related to the seeds making contact with the soil in order to use resources for establishment and growth. Our hypothesis regarding die-off behavior, which they are caused by pathogenic activity in connection with dense litter, was neither supported nor refuted. In addition, our results indicate that die-offs do not follow a specific pattern for recovery following a disturbance.

The fungicide treatment did not have a significant influence either year of the study. Its lack of control of the pathogens may have been due to fungicide breakdown from the time of application, roughly 4-6 weeks, to when the fungi were pathogenic to the seeds. Or the fungicide may not have been active on this isolate of *Fusarium*. Our revised treatment of spraying the plot rather than dipping the seed was applied after the first rainfall that would trigger germination. We hoped to eliminate fungicide breakdown and see increased cheatgrass growth, again it was not observed.

The addition of inoculum to field plots did not effectively replicate anticipated disease levels as predicted and may be due to the use of a *Fusarium* strain that is better suited for warmer temperatures and not the cool fall temperatures. Similar results of temperature dependent Fusarium isolates were also found by Marin, isolates of *Fusarium* from maize had varying germination rates when under different temperature ranges (1996). Our inoculum was applied late in the Fall, similar to the previous year at Dun Glen 2012-2013, and temperatures were not conducive for growth of our *Fusarium* strain (J. Franke personal communication). The use of applying uninoculated oat grain chaff to the entire White Rocks 2013-2014 design eliminated any increased cheatgrass effects of the mulching from the inoculum carrier, which occurred in the previous year's study.

We still do not fully understand why newly establishing cheatgrass had higher emergence in the die-off at Dun Glen and then did not repeat a similar outcome the following year in the cheatgrass monoculture at White Rocks. It is possibly due to the severity or intensity of the die-off condition. The severity of the disturbance could include more depleted seedbanks and higher density of grey matted litter. Both sites contained all of the symptoms of die-off activity, but the parameters in which to distinguish die-off and its level of severity need further research and investigation. There is the possibility that the White Rocks cheatgrass monoculture was healthier, because there was such higher plant count that year (Figure 1D) than Dun Glen cheatgrass monoculture. Overall cheatgrass stand health likely skewed the comparison with the die-off for both sites. It is also possible that natural recruitment and/or the seedbank were stronger in the White Rocks cheatgrass monoculture since plant counts were higher. It could be that the die-off in Dun Glen actually recovered faster than the die-off in White Rocks due to a stronger seed bank or even natural recruitment into the area as well. These reasons could explain why there were contradictory outcomes for emergence variables in both die-off and cheatgrass plots for the study sites.

Die-off recovery areas must follow a cyclical pattern where the disturbance is temporary and the area will eventually become functioning cheatgrass monocultures again, but it is still unclear why some persistent die-offs fail to follow this ecological transition back to full functioning cheatgrass monocultures the following year (Figure 3A-C). Persistent multi-year die-offs possibly eliminate the seed bank of cheatgrass and create stark bare ground areas for reasons that are still not understood. It is assumed that the carryover seed bank of cheatgrass following a die-off event is adequate to reestablish the area, whereas in other scenarios, there are not enough viable seeds to carry over into the following year for successful stand establishment. Failure to

recover post die-off disturbance could be due to unsuitable parameters for the seeds such as poor soil-seed contact, nutrient availability, and poor water relations (Beckstead and Augspurger 2004; Belnap et al. 2003; Thill et al. 1979).

Seed retention on smooth soil surfaces of unrecovered die-offs could be a limiting factor to recovery of a die-off and establishment of cheatgrass seeds. Observations of annual dicot weeds colonizing the persistent die-off bare ground areas are most likely due to efficient dispersal methods such as wind driven dispersal and mucilaginous seeds that allow them to better adhere to smooth soil surfaces (Stallings et al. 1995; Western 2012). Cheatgrass on the other hand, apparently does not employ all of these successful dispersal techniques for bare soils and is less likely to establish or does not disperse to these areas.

It was expected that litter would increase cheatgrass emergence by creating a refuge to hold seeds, but in natural dispersal counts, litter significantly lowered emergence across all treatments in recovering die-offs (Figure 3B). The initial hypothesis was that litter could help trap the dispersed seed and could also aid in increased moisture retention to encourage emergence to create establishment windows as observed in the vegetation and interspaces of sagebrush communities (Chambers et al. 2007). Thus, it is likely that litter present on the plot shielded the dispersed cheatgrass seed from reaching the soil to germinate for natural dispersal counts (Hamrick and Lee 1987). Our hypothesis that the lack of litter would limit cheatgrass establishment and emergence on recovering die-offs has therefore not been supported.

The litter used in our study was autoclaved to kill all pathogens before it was installed onto the field plots. Since our litter treatment did not significantly promote or reduce cheatgrass emergence in recovering die-offs, it is possible that the presence of naturally occurring litter in die-offs might be pathogenically active as it has been shown that litter present on the plot can

reduce cheatgrass establishment in both cheatgrass monoculture and die-off plots (Figure 2A, B). Broadcast cheatgrass seeds were able to establish in litter absent or present plots but more so in the litter absent plots; therefore, die-off disease levels were absent or too low to further restrict cheatgrass emergence and maintain bare ground disturbance post die-off activity. There is still much to learn about these processes, but it is now known that the residual effects of soil-borne pathogens probably play little if any role in the slow recovery of old die-offs because the litter and plants are not there to maintain pathogen populations.

Good seed to soil contact appears essential for effective die-off recovery. Cheatgrass requires environmental conditions less harsh than those of bare soil whereas, other weeds such as Russian thistle and Tumble mustard can establish better on bare soil (Young et al. 1972). When seeds were directly planted into soil of persistent bare ground die-offs, higher proportions of cheatgrass seed established and grew when compared to our broadcast seeds (Figure 3B). Our results were most likely influenced by soil moisture retention and suitable safe sites for plant emergence and growth on direct planted seeds because they were actually planted into the mineral soil rather than suspended on the bare ground.

What is most compelling about the results from the die-off recovery study is that nothing inhibits cheatgrass from establishing following a persistent die-off disturbance. If cheatgrass seeds are added to bare soil in persistent die-off areas, plants will establish. Surprisingly, cheatgrass was successful in establishing with or without the addition of water on bare ground areas of our direct and broadcast treatments.

There was significant natural recruitment from the seed bank or seed dispersal, because the plant count of natural recruitment was higher (8.2 plants/plot) than our broadcast plots (3.7 plants/plot). So when taking into account the natural recruitment that might have occurred within

broadcast seeding plots, 3.7% of our broadcast treatment seeds were actually successful. It is possible that a majority of the plants that established in the broadcast plots could have come from natural recruitment. Cheatgrass seed dispersal on bare soils is 50-fold higher than intact sagebrush ecosystems (Johnston 2011). If seed dispersal were to happen, these persistent die-off areas are more likely to have high cheatgrass seed densities since they lack obstructing vegetation. It can be estimated that seeds are dispersing into these bare ground plots at relatively high densities, as in 100-200 seeds per sqft. These persistent die-offs do not contain a viable seed bank and seed must be dispersed in for recruitment to occur. It is plausible then that seed is the limiting factor for these areas to recover as long as seed production and dispersal from the nearby surrounding intact monocultures is adequate.

Die-off phenomena are still not understood. Environmental variables such as pathogen stimulation and/or appropriate seedbank densities could trigger these epidemic events, and possibly by multiple *Fusarium* strains and other possible pathogens present in the soil. We hypothesize that the reason die-offs do not occur yearly is because of pathogen populations that have dropped or gone inactive and cannot recreate a die-off event because the litter or plant density is not available to trigger pathogenic activity. After a die-off, the thick cheatgrass litter decomposes and the micro-environments for the pathogens are gone because there are no plants, litter, or nutrients so the pathogen populations' decrease and a die-off can return to a cheatgrass monoculture if soil seed contact is favorable. However, if the ground becomes bare too quickly and no cheatgrass seeds remain in the seed bank, then the die-off becomes a persistent die-off.

## IMPLICATIONS

Die-off events present an interesting opportunity in the reestablishment and restoration of natives. Since there are no intrinsic factors that inhibit the establishment of cheatgrass post die-off disturbance, it is plausible that a unique window is available for land managers to revegetate natives in invasive weed populations as large quantities of cheatgrass seeds fail to emerge during die-off events. Research is underway on the ability of native seeds to establish in die-offs (Baughman 2014). However, die-offs can also exhibit environmental hazards if not properly managed. Die-off areas, which can be very large at times, are void of stable cheatgrass roots whereupon soil instability and erosion can prevail. Die-off's can also pose a threat to air quality and foster ecosystem degradation and desertification. Grazing too is affected by the lack of new plant establishment as it is possible for vast areas of forage to disappear unexpectedly. The transient nature of die-off and the unpredictability of its occurrence and duration are alarming yet as more is understood about this phenomenon it is possible to harness these disturbances as an option for native revegetation. It is imperative to understand the components of die-off, so that we can better manage and sustain fragile desert ecosystems and reduce cheatgrass invasion.

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# TABLES

**Table 1.** Short-Term Recovery Experimental Design.

| | Dun Glen, NV | White Rocks, UT | | |
|---|---|---|---|---|
| **Site** | | | | |
| **Treatments** | Litter +/- | Inoculum / Fungicide | Die-off / Cheatgrass | Water +/- |
| **Layout** | 20 Block | 240 Plots | | |
| **Seeds** | 20 seeds/plot | 4800 total glued | | |
| **Installation Dates** | Layout August 2013 (White Rocks) | Full Installation October 2012 (Dun Glen) September 2013 (White Rocks) | Fungicide October 2013 (White Rocks) | |

**Table 2**. Long-Term Recovery Experimental Design.

| | | | |
|---|---|---|---|
| **Site** | White Rocks, UT | | |
| **Treatments** | Litter +/- | Water +/- | Direct / Broadcast |
| **Layout** | 10 Block | 80 Plots | |
| **Direct Seed** | 20 seeds/plot | 4800 glued | |
| **Broadcast Seed** | 100 seeds/plot | 4000 seeds | |
| **Installation Dates** | Layout<br>August 2013 | Full installation<br>October 2 2013 | |

**Table 3.** Dun Glen Experimental Design for Short Term Die-Off Study.



CHEATGRASS MONOCULTURE
10 Blocks
12 Treatments/block
120 Plots
Treatments: Litter, Inoculum,
Fungicide, Water

DIE-OFF
10 Blocks
12 Treatments/block
120 Plots
Treatments: Litter, Inoculum,
Fungicide, Water
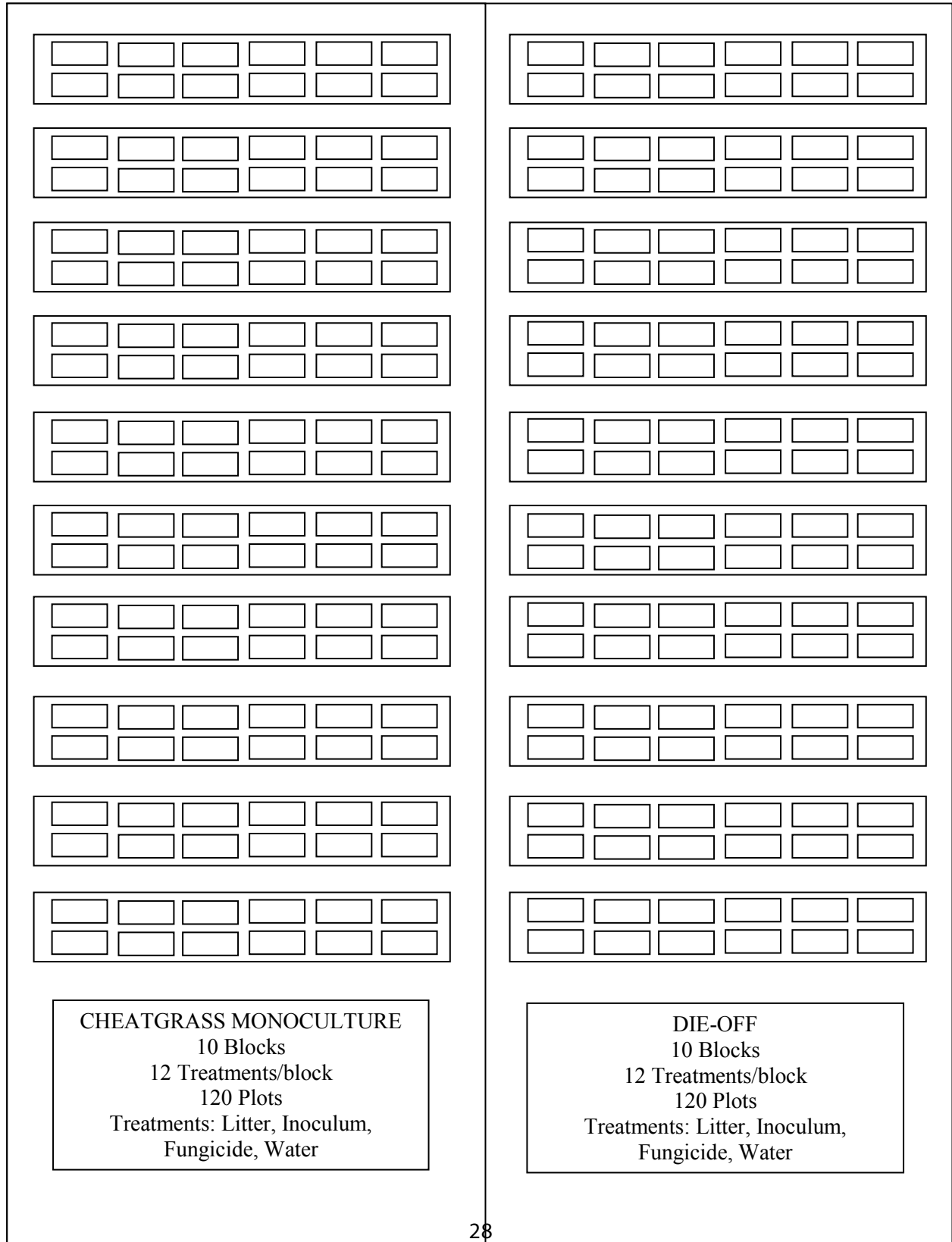
**Table 4.** White Rocks Experimental Design for Short Term Die-Off Study.



| Control | Inoculum | Fungicide |
| --- | --- | --- |

CHEATGRASS MONOCULTURE
10 Blocks
12 Treatments/block
120 Plots
Treatments: Litter, Inoculum, Fungicide, Water
All sub-sub [L, W] plots within sub plots [C, I, F]

| Control | Inoculum | Fungicide |
| --- | --- | --- |

DIE-OFF
10 Blocks
12 Treatments/block
120 Plots
Treatments: Litter, Inoculum, Fungicide, Water
All sub-sub [L, W] plots within sub plots [C, I, F]

29
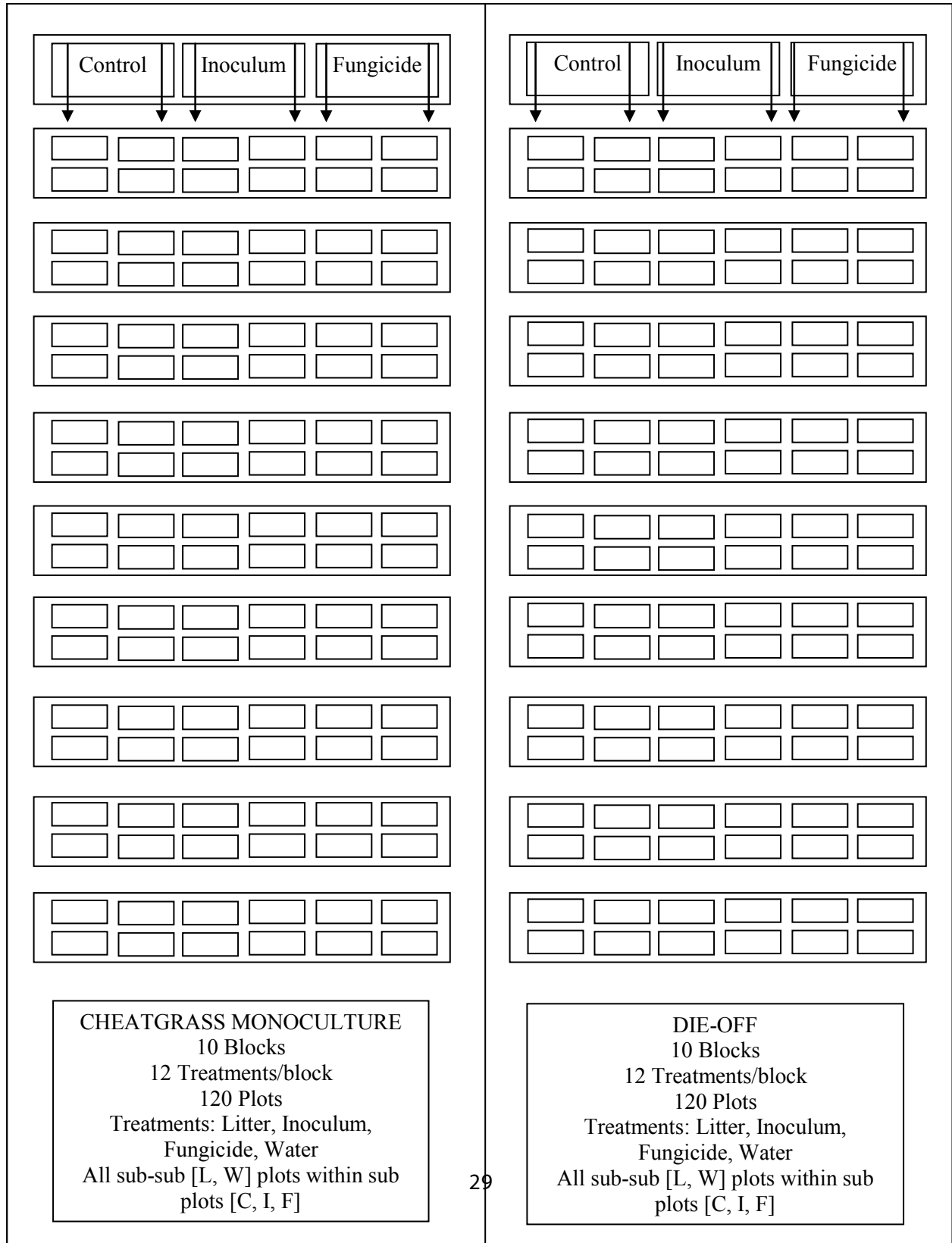
**FIGURES**



**Figure 1A-D**. Percent emergence [A], percent survival [B], biomass (g) [C], and plant count [D] was measured in die-off field trials in Dun Glen 2012-2013 and White Rocks 2013-2014. Treatments include die-off vs cheatgrass (established monoculture cheatgrass stand), data were collected from all plots across the study. For comparing die-off and cheatgrass, bars with the same letter within the same location are not significantly different at $P < 0.05$. Percent emergence and survival includes experimental plants. Plant count and biomass includes all plants from both natural recruitment and experimental within the plot.
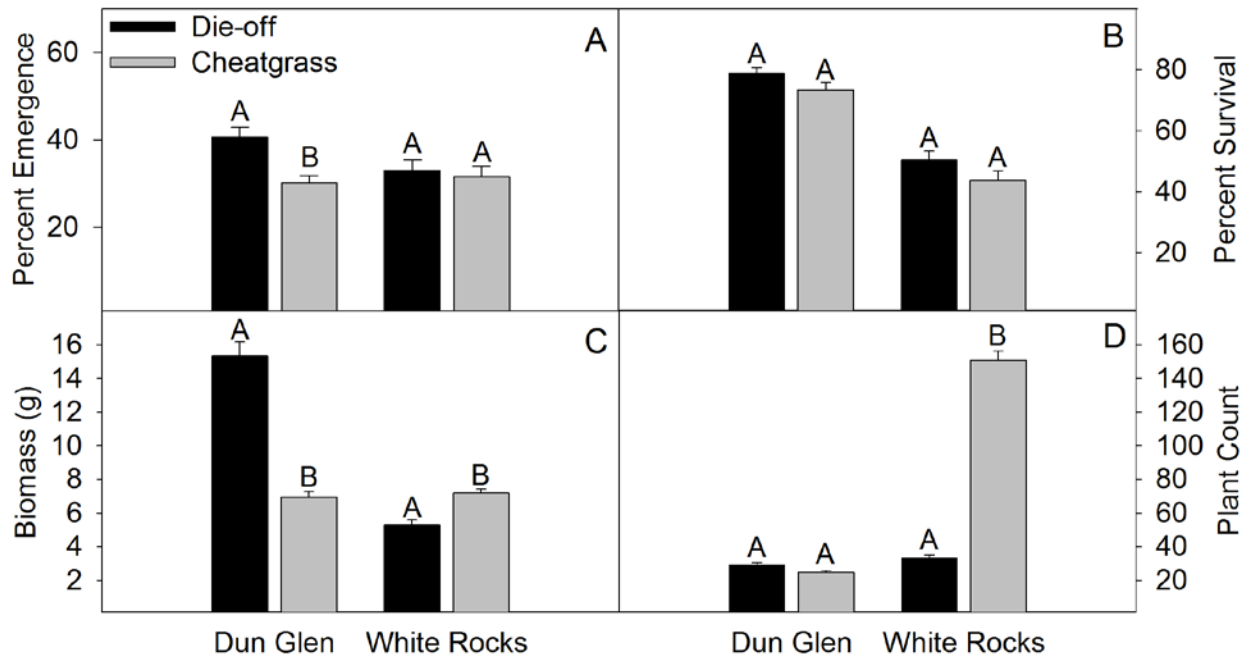
**Figure 2A-D.** Percent emergence [A], percent survival [B], biomass (g) [C], and plant count [D] was measured in die-off field trials in Dun Glen 2012-2013 and White Rocks 2013-2014. Treatments include litter present and absent, data were collected from sub plots across the study. Percent emergence and survival includes experimental plants. For comparing litter present and litter absent, bars with the same letter within the same location are not significantly different at P < 0.05. Percent emergence and survival includes experimental plants. Plant count and biomass includes all plants both natural recruitment and experimental within the plot.
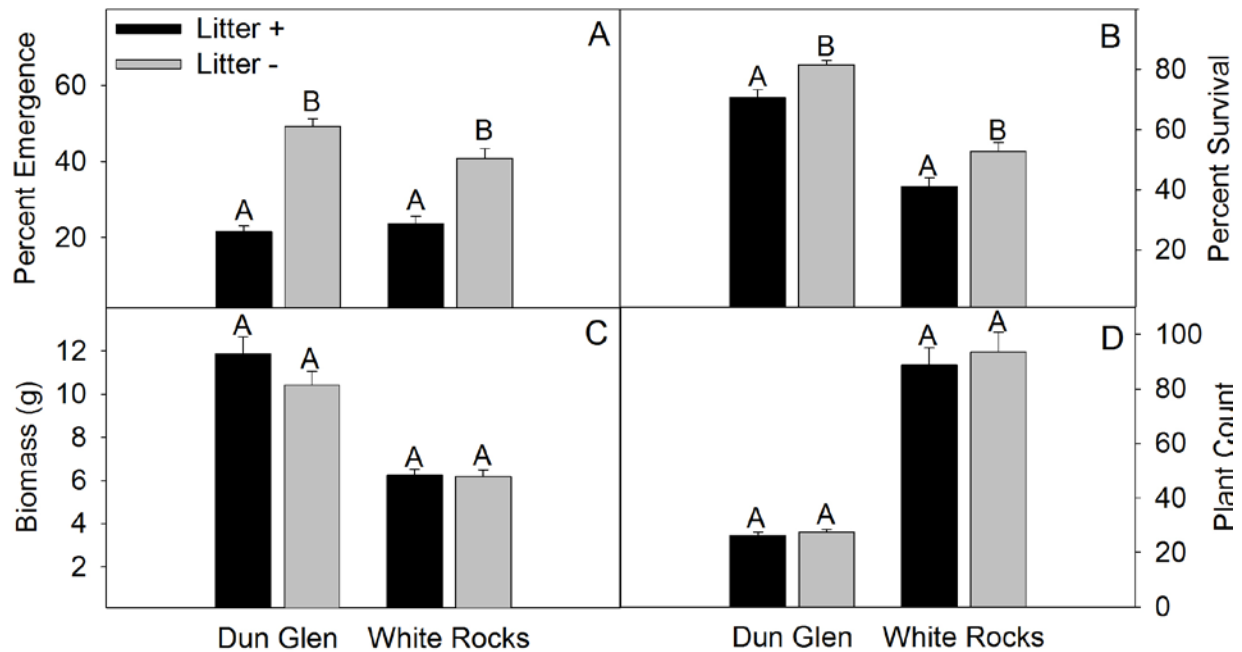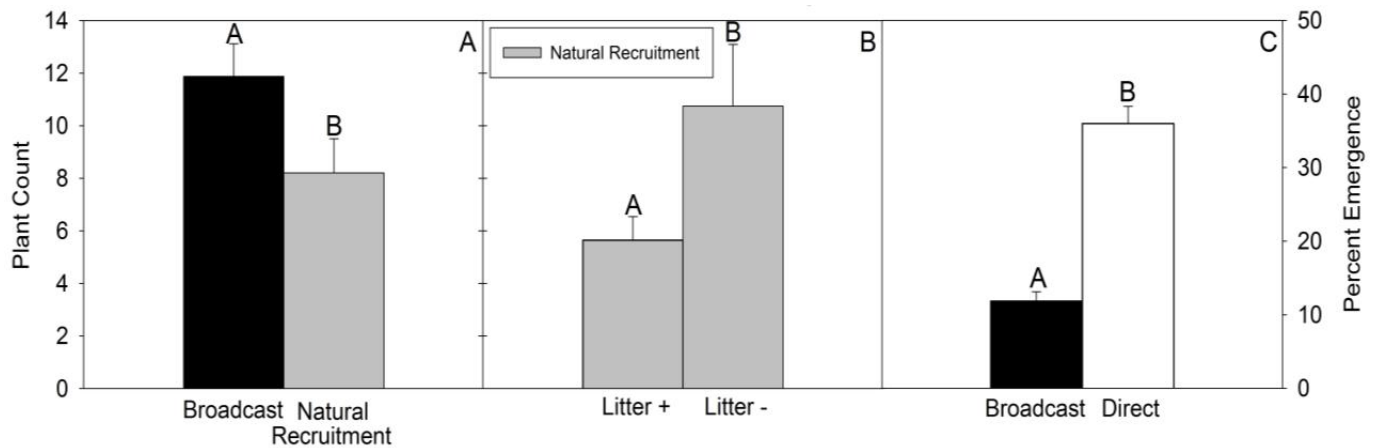
**Figure 3A-C.** Total emergence proportion and plant count was measured in die-off recovery field trials in White Rocks 2013-2014. Treatments include natural recruitment and broadcast [A]. Litter present and absent are within natural recruitment plots [B] and the y axis is present on the far left of graph [A]. Treatments include direct vs broadcast seeding placement [C] the y axis is on the right.

**APPENDIX**

**Table 1.** Anova Table for Dun Glen Short-Term Study for Percent Emergence.

| Source of Variation | DF | SS | MS | F | P |
|---|---|---|---|---|---|
| Condition | 1 | 0.732 | 0.732 | 21.515 | 5.86e-06 |
| Water | 1 | 0.072 | 0.072 | 2.111 | 0.148 |
| Litter | 1 | 4.551 | 4.551 | 133.859 | < 2e-16 |
| Disease | 3 | 0.061 | 0.020 | 0.594 | 0.619 |
| Residual | 233 | 7.992 | 0.034 | | |

**Table 2.** Anova Table for Dun Glen Short-Term Study for Percent Survival.

| Source of Variation | DF | SS | MS | F | P |
|---|---|---|---|---|---|
| Condition | 1 | 0.0021 | 0.0021212 | 1.171 | 0.280 |
| Water | 1 | 0.0003 | 0.0002699 | 0.149 | 0.700 |
| Litter | 1 | 0.0000 | 0.0000001 | 0.000 | 0.995 |
| Disease | 3 | 0.0042 | 0.0013934 | 0.769 | 0.512 |
| Residual | 233 | 0.4220 | 0.0018110 | | |

**Table 3.** Anova Table for Dun Glen Short-Term Study for Biomass.

| Source of Variation | DF | SS | MS | F | P |
|---|---|---|---|---|---|
| Condition | 1 | 4217 | 4217 | 99.738 | < 2e-16 |
| Water | 1 | 866 | 866 | 20.4483 | 9.61e-06 |
| Litter | 1 | 119 | 119 | 2.815 | 0.0947 |
| Disease | 3 | 148 | 49 | 1.166 | 0.3234 |
| Residuals | 232 | 9808 | 42 | | |

**Table 4.** Anova Table for Dun Glen Short-Term Study for Plant Count.

| Source of Variation | DF | SS | MS | F | P |
|---|---|---|---|---|---|
| Condition | 1 | 1247 | 1246.6 | 10.539 | 0.001349 |
| Water | 1 | 82 | 82.0 | 0.693 | 0.405898 |
| Litter | 1 | 85 | 85.4 | 0.722 | 0.396338 |
| Disease | 3 | 2461 | 820.3 | 6.935 | 0.000175 |
| Residuals | 223 | 26378 | 118.3 | | |

**Table 5.** Anova Table for White Rocks Short-Term Study for Percent Emergence.

| Source of Variation | DF | SS | MS | F | P |
|---|---|---|---|---|---|
| Condition | 1 | 0.012 | 0.0123 | 0.206 | 0.650 |
| Water | 1 | 0.005 | 0.0051 | 0.085 | 0.771 |
| Litter | 1 | 1.910 | 1.9102 | 32.056 | 4.39e-08 |
| Disease | 2 | 0.107 | 0.0535 | 0.898 | 0.409 |
| Residuals | 233 | 13.884 | 0.0596 | | |

**Table 6.** Anova Table for White Rocks Short-Term Study for Percent Survival.

| Source of Variation | DF | SS | MS | F | P |
|---|---|---|---|---|---|
| Condition | 1 | 0.00345 | 0.003449 | 2.651 | 0.1048 |
| Water | 1 | 0.00057 | 0.000567 | 0.436 | 0.5097 |
| Litter | 1 | 0.00381 | 0.003815 | 2.932 | 0.0882 |
| Disease | 2 | 0.00122 | 0.000610 | 0.469 | 0.6264 |
| Residuals | 233 | 0.30316 | 0.001301 | | |

**Table 7.** Anova Table for White Rocks Short-Term Study for Biomass.

| Source of Variation | DF | SS | MS | F | P |
|---|---|---|---|---|---|
| Condition | 1 | 211.3 | 211.29 | 22.001 | 4.64e-06 |
| Water | 1 | 0.0 | 0.01 | 0.001 | 0.981 |
| Litter | 1 | 0.4 | 0.39 | 0.041 | 0.840 |
| Disease | 2 | 39.0 | 19.48 | 2.029 | 0.134 |
| Residuals | 233 | 2237.6 | 9.60 | | |

**Table 8.** Anova Table for White Rocks Short-Term Study for Plant Count.

| Source of Variation | DF | SS | MS | F | P |
|---|---|---|---|---|---|
| Condition | 1 | 820458 | 820458 | 421.292 | <2e-16 |
| Water | 1 | 2 | 2 | 0.001 | 0.973 |
| Litter | 1 | 1129 | 1129 | 0.580 | 0.447 |
| Disease | 2 | 5710 | 2855 | 1.466 | 0.233 |
| Residuals | 231 | 449868 | 1947 | | |

**Table 9.** Anova Table for White Rocks Bare Ground Study for Direct Seeded Treatments with

Percent Emergence.

| Source of Variation | DF | SS | MS | F | P |
|---|---|---|---|---|---|
| Litter | 1 | 1.600 | 1.600 | 0.183 | 0.672 |
| Water | 1 | 19.600 | 19.600 | 2.239 | 0.143 |
| Litter x Water | 1 | 4.547E-013 | 4.547E-013 | 5.194E-014 | 1.000 |
| Residual | 36 | 315.200 | 8.756 | | |

**Table 10.** Anova Table for White Rocks Bare Ground Study for Seeding Placement Treatments with Plant Count.

| Source of Variation | DF | SS | MS | F | P |
|---|---|---|---|---|---|
| Seeding | 2 | 630.113 | 315.056 | 5.057 | 0.009 |
| Litter | 1 | 144.208 | 144.208 | 2.315 | 0.133 |
| Water | 1 | 36.939 | 36.939 | 0.593 | 0.444 |
| Residual | 68 | 4236.550 | 4236.550 | | |

# MAPS

**Map 1.** Dun Glen Site using imagery from Google Earth.
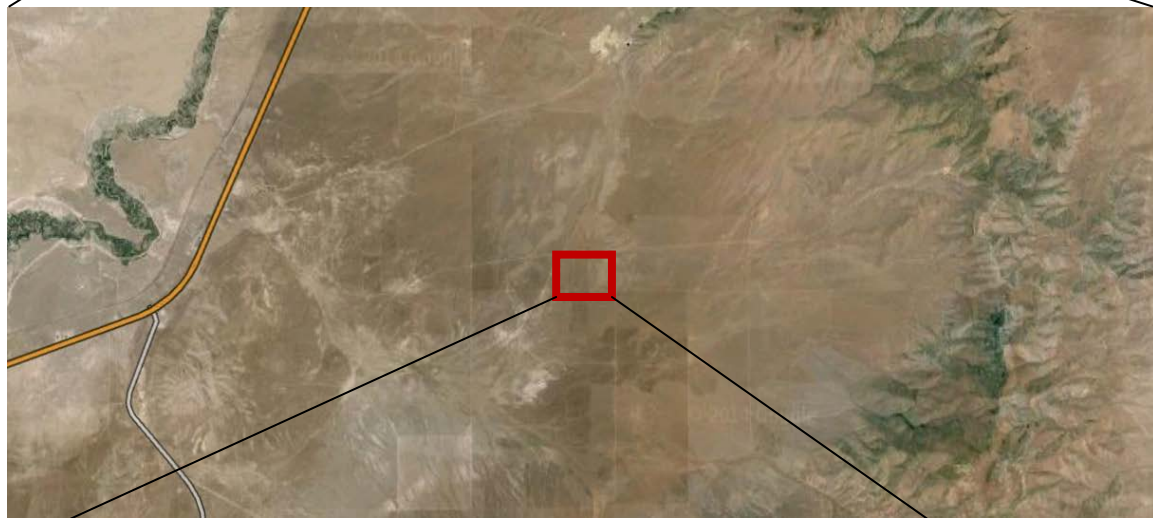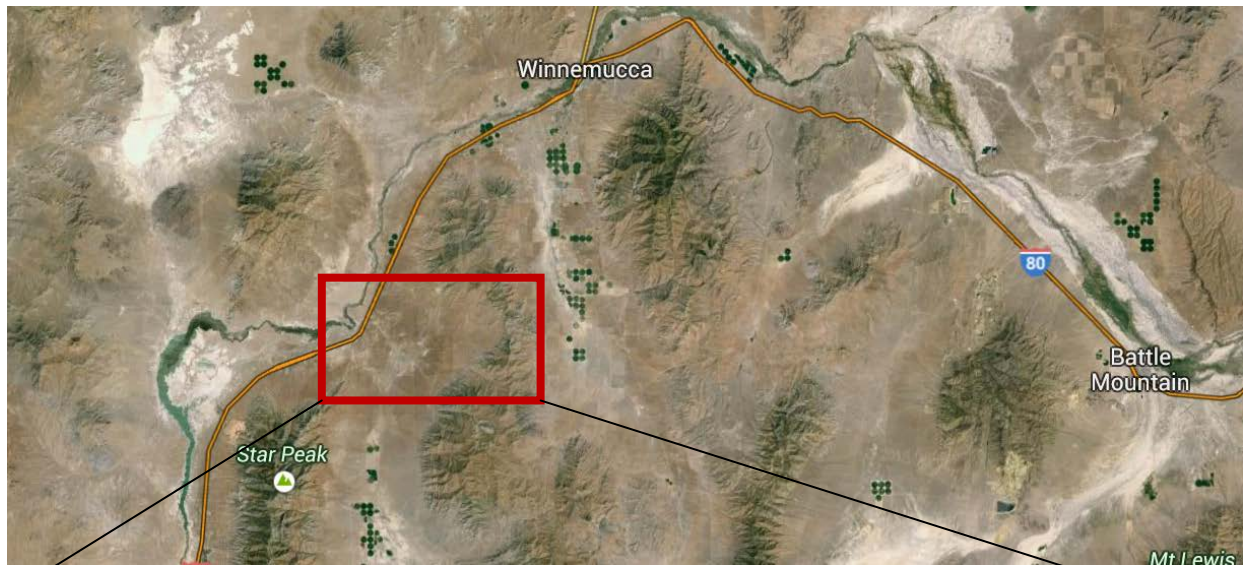


Dun Glen site south of Winnemucca, Nevada.

**Map 2.** White Rocks Site using imagery from Google Earth.



White Rocks site north of Dugway, Utah.