

AN ABSTRACT OF THE THESIS OF

Ryan Leary for the degree of Master of Science in Rangeland Ecology and Management presented on June 20, 2008.

Title: Winterfat Seed Viability and Dormant Season Livestock Grazing

Abstract approved:

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Krascheninnikovia lanata (winterfat) is a valuable forage species with an average of 10% crude protein during winter when there are few nutritious options for livestock and wildlife. However, excessive grazing throughout the west has negatively impacted survival of winterfat stands. We hypothesized that four years rest from dormant season livestock grazing, along with rest from antelope and rabbit browse, would result in greater seed viability and aboveground biomass relative to grazed plots.

In locations across the Catlow Valley, Oregon with winterfat communities, two 40 x 40 m plots, a control and an enclosure, were established at each of 15 locations divided among three pastures: north, middle and south. The control plot could be grazed by livestock and wildlife in all seasons (although cattle were only in the study area during the dormant season). The second plot at each location was a large animal enclosure that prevented grazing by cattle and antelope. At four locations a cattle/antelope/rabbit enclosure was also installed. This total of 34 plots was used to test the effects of location and type of use on winterfat seed viability and aboveground plant biomass.

Four years rest from dormant season grazing did not affect the viability of winterfat seed or the levels of aboveground winterfat biomass; however, location across the study area did affect the levels of winterfat aboveground biomass. There

was significant variation in the data attributable to unknown factors but represented by the influence that pasture location had on seed state (viable, dead and empty) and winterfat plant biomass. In the most productive locations, increases in winterfat aboveground biomass were correlated with increases in seed viability and decreases in density of winterfat m^2 while increases in winterfat seed viability were correlated with decreases in the percentage of empty seed. In the locations with the highest levels of dead seed, increases in dead seed were correlated with increases in winterfat density m^2 and decreases in empty winterfat seed.

Plants in the cattle/antelope/rabbit exclosures had the highest winterfat density, the lowest plant biomass, lower levels of empty seed and the highest level of dead seed, the reverse of the most viable plots in the study area. From observation, these plants have a greater amount of woody base growth from prior years and appear more decadent. Further research is needed to see if winterfat seed viability and biomass production is associated with some level of browse. Nuttall's saltbush is the dominant shrub on the site, and its increase is correlated with increases in winterfat aboveground biomass and decreases in the level of dead winterfat seed.

These results suggest that resources which vary by pasture location such as precipitation, soil nutrients, texture, or moisture holding capacity determined levels of winterfat aboveground plant biomass, winterfat seed state, and the density of Nuttall's saltbush and that on high resource sites, winterfat allocates resources to existing plants in rather than creating the new individuals

The lack of response to four years rest from dormant season grazing, the low levels of viable seed, the low density of winterfat, and the encroachment of Nuttall's saltbush all suggest reduced vigor of winterfat in this study area. One possible explanation is that, since recovery toward a later successional stage would be expected with reduced grazing pressure (Dyksterhuis 1949), these arid lands are significantly degraded by stress or disturbance (Westoby et al. 1989; Laycock 1991) and that recovery is no longer possible without significant intervention. This suggests that the study area has crossed an ecological threshold. An alternate possibility is that since

recruitment of winterfat is episodic and driven by precipitation events, climatic fluctuations may have prevented the sequence of good precipitation years needed for stand maintaining winterfat recruitment (Pechanec 1964). Further study is needed to evaluate these possibilities.

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Winterfat Seed Viability and Dormant Season Livestock Grazing

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Dr. Tamzen Stringham aided in experimental design, field sampling methods, data analysis, interpretation and discussion of the data and edited all chapters.

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CHAPTER 1: GENERAL INTRODUCTION

Krascheninnikovia lanata (winterfat) is a valuable forage species with an average of 10% crude protein during winter when there are few nutritious options for livestock and wildlife (Welch 1989). However, several studies suggest that excessive grazing throughout the west has negatively impacted survival of winterfat stands (Hilton 1941; Statler 1967; Stevens et al. 1977). In the Catlow Valley of southeast Oregon local ranchers have observed this decline in dormant season grazed winterfat stands and are anxious to reverse it. Many factors could be contributing to the decline related to plant ecology, climatic factors, stress, or disturbance.

WINTERFAT ECOLOGY AND ENVIRONMENTAL PREFERENCES

Winterfat is a long-lived native shrub typically about 30 cm tall (Mozingo 1987). It has a woody base from which annual branchlets grow (Welsh et al. 1987). The most common variety is a low growing dwarf form (less than 38.1 cm), which is most often found on desert valley floors (Stevens et al. 1977). Winterfat is commonly found on desert ranges with less than 10 inches (25.4 cm) of precipitation. It tolerates a wide range of precipitation, from lows of 4 inches (10.2 cm) to subalpine zones with as much as 40 inches (102 cm) (Stevens et al. 1977). Winterfat is adapted to a broad range of elevations and temperatures. It grows at sea level (Death Valley) up to 10,000 feet (3,048 m) (central Utah mountains) (Stevens et al. 1977) and in the Desert Experimental range in SW Utah at elevations from 5,075 (1547 m) to 8,415 feet (2,565 m) (Clary and Holmgren 1982). Winterfat grows throughout the Great Basin from the lower Sonoran zone to ridges over 3,048 m in elevation. Winterfat is common over the Great Basin in shadscale-greasewood associations. In the north it is found with saltbush, rabbitbrush, sagebrush, and greasewood; in the south it is found in mesquite communities (Mozingo 1984).

Winterfat is found in a wide range of soil types, from clays to sandy and rocky loams (Booth 2006). In a cold desert community of the Desert Experimental Range in Pine Valley in western Utah, it grows in gravelly and sandy loams (Duda et al. 2003). In Utah's Ouray National Wildlife Refuge, it grows in silty clay soils (USFWS 2005). In New Mexico, it grows in sandy loams and clay loams that can be cherty, stony, gravelly, or rocky (Woodmansee and Potter 1971). Winterfat prefers soils high in pH and carbonates and low in soluble salts and in exchangeable sodium (Riedl et al. 1964).

Soil texture and structure influence the speed and amount of infiltration as well as the water-holding capacity of the soil, dictating the amount of water available to roots for plant growth (Gates and Cook 1956). Coffin and Lauenroth (1992) found that soil texture (coarse or fine) and clay content influenced the number of seeds produced by *Bouteloua gracilis*; Spaeth et al. (2007) found that the vegetation, plant composition, and soil physical properties varied with the hydrology of microsites (shrub coppice, shrub dripline, and varying distances along the interspace) in a mountain big sagebrush community. Sala et al. (1988) found that two variables, annual precipitation and soil water holding capacity, accounted for the variability in production at their central grassland site. Goodman (1973) found that soil nutrients and salinity affected the growth of winterfat, which decreased with increased salt and boron, and Nuttall's saltbush, which increased with increased salt and boron. Westoby et al. (1989) described the transition caused by wind erosion of the topsoil where the site became an unvegetated claypan. Studies attempting to isolate edaphic factors in winterfat-artemesia-atrilex communities which predict where winterfat will grow have not been successful in identifying clear edaphic or environmental indicators (Gates et al. 1956; Mitchell et al. 1966).

Winterfat varies its annual growth cycle based on latitude, elevation and precipitation. Winterfat growing in south central Idaho completed its above ground growth between March and October (Windle 1960). Average seasonal growth in the Curlew Valley in northern Utah began somewhat later, in early- to mid-April (West

and Gasto 1978). Total winter precipitation is a primary growth driver, and lower than average spring precipitation can reverse the impact of plentiful winter precipitation. While summer rainfall has a limited impact, heavy August-September rain can cause a second flowering in winterfat (West and Gasto 1978).

Winterfat has a deep taproot supplemented by fibrous branched lateral roots. These are primarily in the upper meter of soil, but roots may go as deep as 145 cm (Stevens et al. 1977). Typically, winterfat's belowground biomass is 11 times the aboveground, enabling it to survive in low precipitation environments. This high root:shoot ratio, coupled with its ability to regenerate its fibrous root system to continually seek out water, enables winterfat to be photosynthetically active in all but the driest months of the year (Caldwell and Camp 1974).

Density and vegetative production of winterfat varies by site. In an *Agropyron-Koeleria* Faciation¹ in the Mixed Prairie in Saskatchewan where the mean annual precipitation averages 12.9 inches (326 mm) and average temperature ranges from 6°F (-14.5 C) in the winter to 66°F (18.8 C) in the summer, average density of winterfat protected from grazing was 1.1 plants m² and 0.5 m² in the pasture grazed from May to October. Annual growth biomass on control plants averaged 11.7 grams and those defoliated averaged 7.3 grams (Romo et al 1995). Average annual winterfat production in three Nevada locations was 194 pounds per acre (22 g m²). Production was correlated with annual winterfat plant growth and was greatest in the summer (Kinsinger and Strickler 1961). Coyne and Cook (1970) found that winterfat growth rate, like that of other desert range species, is directly related to soil moisture.

WINTERFAT REPRODUCTION

Winterfat adapts its bloom period to the elevation and weather, blooming from June to August in response to local site conditions (Stevens et al. 1977). Its inflorescence is a gray green spike, and the flowers are either staminate comprised of a 4-part calyx with 4 exerted stamens or pistillate with 2 united bracts each supporting 2

¹ A climax association which lacks some of the dominants of the normal association.

styles (Booth 2006). Winterfat plants can be monoecious with staminate flowers above the pistillate flowers, or they can be dioecious (Stevens et al. 1977; Mozingo 1987).

The embryo of winterfat fruits is attached to the cotyledons with the radicle at the center. The embryo is enclosed with the perisperm (food storage tissue) in the testa (seed coat) forming the seed. The seed is enclosed by the pericarp, forming the utricle, which is in turn enclosed by two united bracts, forming a bract wall. Bracts are tufted and form a silky covering at maturity (Booth 1989). Fruits measure 5 to 8 mm in length and 3 to 5 mm in width depending on ecotype, and plants produce between 25,000 and 125,000 fruits per pound, depending on the collection area and the degree of fill (Stevens et al. 1977). The percentage of fruits with filled seeds varies widely; in a group of five different New Mexico seed collections, the percentage of fruits with filled seeds ranged from 67% to 95 % (Springfield 1974).

Winterfat reproduces from seed and primarily pollinates via wind, either between plants, or, on monoecious plants, within the same plant (Stevens et al. 1977). Winterfat has multiple dispersal mechanisms: diaspores are shed in the fall or winter, dispersed by wind, rodent-cached, or carried on animals (Majerus 2003). Diaspores take advantage of available moisture, tolerating freezing conditions as they progress from imbibed seeds to germinants to nonwoody seedlings (Booth 1987). Under some circumstances, the degree of reproduction may be density dependent. Freeman and Emlen (1995) found that winterfat exhibited a strong Allee effect, with per capita reproduction declining at low plant densities.

Stand maintaining or stand increasing winterfat seed production requires adequate summer rainfall and rest from summer grazing. If these conditions are absent, winterfat plants may not produce seed in any given year (Stevens et al. 1977). Seed production and regrowth are curtailed if grazing occurs as the plant begins to grow (Eckert 1954). In general, larger plants produce more seed (Freeman and Emlen 1995), and larger seeds germinate at higher rates (Springfield 1973). The presence of other plants, including *Bromus tectorum*, *Hilaria jamesii*, and *Halogeton* has been found to negatively impact seed production (Freeman and Emlen 1995; Hild 2007).

The amount of seed winterfat plants produce depends on a number of factors including site conditions, plant size, and the number of fruits that are filled with seed. Stevens et al. (1977) reported that in Utah, in a collection of whole fruits, the number of fruits per kg ranged from 55,125 to 275,625, and in another collection, when seed had been threshed from the fruits, the average number of seeds per kg varied from 24,696 to 551,250. Springfield (1974) found the fill rate of winterfat fruits collected at five sites in New Mexico varied from 67% to 95% among the five collections. The variation in degree of fill has been characterized by Stephenson (1981) as a strategy of outcrossing plants which overproduce flowers and subsequently abort the immature fruits in order to disperse pollen while matching actual fruit production to available resources. Winterfat seed production is highly correlated with plant size, with larger plants producing more seed (Freeman and Emlen 1995). Pechanec (1964) emphasized the importance of above average precipitation for both the production of seed and the subsequent establishment of seedlings, indicating that the combination was infrequent in the arid west.

Winterfat seed viability is a product of the environmental conditions during seed formation and of the physiological characteristics of the seed (Woodmansee and Potter 1971). A seed contains the embryo and food reserves whose quality is determined by the mother plant's allocation of carbon and nutrients to reproduction (Lambers et al. 1998). Maternal resources committed to winterfat seeds are one of the determinants of viability and early seedling growth. This allocation to reproduction varies depending on environmental conditions the mother plant is experiencing during seed formation and typically represents from 1% to 30% of the allocation to net primary production (Lambers et al. 1998). The level of calcium ions (Ca^{++}), which strongly affects seedling vigor, is determined by mother plant transpiration. Mother plant nutrition determines the levels of potassium ions (K^+) and sodium ions (Na^+) available in the seed to support seedling growth. Na^+ is particularly important because it is correlated with greater hypocotyl length in seedlings (Booth 1990). Moisture absorption by the seed is improved by increased Ca^{++} or by increased Na^+ (Booth

1989). The presence of these salts in the bracts and seeds also depresses the freezing point, allowing winterfat to better tolerate below-freezing temperatures as it germinates (Booth 1987). Higher concentrations of glucose, raffinose, and sucrose correlate with better cold tolerance in the seed (Wang et al. 2006b). When the mother plant commits fewer resources and creates a smaller seed, those seeds are more sensitive to external conditions and less likely to produce seedlings (Springfield 1973). Climatic stressors on the mother plant reduce its ability to produce viable seed. High wind speeds can cause the stomata to close and interrupt photosynthesis, resulting in seed with decreased offspring vigor (Booth 1990). Drought conditions have a significant impact on seed production. In years of lower precipitation, particularly in the winter, plants have truncated reproductive phases with low or no seed set (West and Gasto 1978).

Seed viability is measured for both winterfat fruits and for winterfat seeds threshed from the fruit. In a New Mexico field study, Booth and Shuman (1983) found 49% viability as measured by germination rate in a sample of winterfat fruits and 97% viability as measured by germination rates for threshed seed. Riedl et al. (1964) tested winterfat threshed seed from 6 sites in Wyoming and found threshed seed viability as measured by germination rate ranged from an average of 47% to 78%. Springfield (1968) tested threshed winterfat seed across two sites in New Mexico and found viability as measured by germination rate ranged from 60% to 70%.

Temperature fluctuations can decrease winterfat viability. Dettori et al. (1984) found viability as measured by germination rate for northern Utah threshed seed subjected to alternating temperature regimes varied between 23% and 35% for seed incubated four weeks, while the Hatch cultivar in the same study had a viability range as measured by germination rate from 35% to 46%. For a given sample of winterfat seed, the size of the seed affects the level of viability. Springfield (1973) found that threshed winterfat seed viability as measured by germination rate varied by size class from 99.0% for large seeds to 87.2% for small seeds.

Winterfat can germinate over a range of temperature and moisture conditions once after-ripening is completed. The after-ripening period is at least 9 weeks (Springfield 1972). Optimum germination has been found with soil moisture conditions at field capacity and temperatures ranging from 50⁰ F to 86⁰ F (10 C to 30 C). However, it can germinate at relatively low temperatures and can adapt to moisture stress in narrower temperature ranges. Hydrated seeds can survive freezing to -30 C and still germinate, although at lower rates and with less seedling vigor (Bai et al. 1998). Springfield (1968a) found that winterfat will germinate under moisture stress if the temperature is at or near 41⁰ F. Hilton (1941) found that after germination, winterfat seedlings will survive at temperatures as low as 12° F (-11.1 C). However, in warmer weather, moisture stress decreases germination (Springfield 1968). Winterfat, with its thin seed coating and preformed cotyledons and root radicle, is designed for rapid germination and emergence, suggesting that it can establish rapidly when conditions are favorable. The drawback of this strategy is that the seed is not viable for long. Springfield (1968b) found viability in winterfat seed for up to 3 years. Hilton (1941) found germination of the current year seed to be 97%, 87% in 1-year-old seed, 23.5% in 2-year-old seed, and little germination in 3- and 4-year-old seed.

Seed condition is a predictor of germination, with germination rates and seedling size increasing with seed weight (Hou 1998; Springfield 1973). Results from seedlings provide insight into factors that may contribute to successful natural establishment. Shallow seeding, which is consistent with wind dispersal, is required. Springfield (1971) found that seed spread on the soil surface produced the best results; he also found that a 1/16-inch (1.5 mm) planting depth had maximum emergence. Booth and Schuman (1983) and Woodmansee and Potter (1971) recommend planting at a depth of one-fourth inch (6 mm) or less. Bracts appear to contribute to seedling success. Booth and Schuman (1983) show that threshed seed has higher germination and but lower establishment. Stevens et al. (1977) cite the bracts as important in protecting the seed and reducing precocious germination.

WINTERFAT RESPONSE TO STRESS & DISTURBANCE

Winterfat is a long-lived native shrub that tolerates environmental stress, extremes of temperature and precipitation, and competition from other perennials but not the disturbance of fire or overgrazing (Ogle 2001).

Drought

Winterfat is considered a drought tolerant plant (Stevens et al. 1977), and this is born out by the reports of Chambers and Norton (1993) on their study during a 2-year drought on the Desert Experimental Range in southwestern Utah. They evaluated the performance of winterfat (natality, mortality, and population turnover) as part of a study of dominant salt desert shrub species under different grazing regimes during the drought of 1975-1977. Study treatments included light (20%-50% utilization) to heavy (75% utilization) grazing and the cessation of grazing before active physiological growth of cool season species in late February. During the drought, winterfat had both low mortality and low natality, and there was no difference between grazing treatments.

Competition

Comparing carbohydrate reserves of winterfat and Nuttall's saltbush, Coyne and Cook (1970) found that saltbush reserves were two times higher at all stages of growth. In a southeastern Utah study, West and Ibrahim (1968) found that Nuttall's saltbush replaced climax community shrubs where erosion had occurred in the top three soil horizons. In comparison to Nuttall's saltbush, winterfat is preferentially grazed by cattle. Turner (1971) found that winterfat had 53% use, while Nuttall's saltbush had 22% use.

Freeman and Emlen (1995) studied the competitive impact on plant size and seed set. They found that *Bromus tectorum*, *Chrysothamnus Greenei*, *Aristida purpurea* and *Artemisia spinescens* negatively impacted winterfat plant size while *Salsola kali* and *Descurainia pinnata* had a positive influence in the moderately

(50%) grazed area and a negative influence in the other more heavily (80%) grazed areas. While several species negatively impacted winterfat plant size, only the long-lived perennial rhizomatous grass *Hilaria jamesii* and *Halogeton* negatively impacted winterfat's seed set. Hild et al. (2007), at the Snake River Birds of Prey National Conservation Area in southwestern Idaho, tested winterfat seed from four sources (Birds of Prey, northeastern New Mexico, Northern Cold Desert Select Germplasm, and Open Range Tested Germplasm) in the presence of *Bromus tectorum* and found that for all sources, winterfat growth was depressed by at least 90%.

Herbivory

Time of grazing is critical for winterfat. Romo (1995), in a study in the northern Mixed Prairie of Saskatchewan, found that grazing during its growth period caused the decline of winterfat. He found that plants defoliated in May were able to recover and produce the same level of growth the following year, but plants defoliated in June, July, or August produced the less biomass the following year.

In addition to grazing by cattle, winterfat is browsed by rabbits, antelope, and other wildlife species (Ogle et al. 2001; Stevens et al. 1977). Winterfat and perennial grasses average 80% of the jackrabbits' diet in southeastern Idaho, with shrubs being grazed in fall and winter particularly (Johnson and Anderson 1984). Pronghorn and rabbits browse stems, leaves, and seed stalks of winterfat year round, especially during periods of active growth (Stevens et al. 1977). Browse provides about 64% of the pronghorn diet; winterfat is a secondary shrub for pronghorn, less desirable than sagebrush and saltbrush (USDA 1971).

Shrubs are the primary winter feed of blacktailed jackrabbits, and during population highs they can cause considerable damage to rangeland vegetation (McAdoo 2002). In addition to damaging stands, rabbits may destroy winterfat seedlings (Ogle et al. 2001). An Idaho study found that, at their cyclical high density, black-tailed jackrabbits had completely eaten most aboveground forage by spring. The

plants recovered by July, and at that point there was no difference between plants in grazed and protected plots (Anderson 1986).

WINTERFAT RESPONSE TO GRAZING

Winterfat response to grazing varies based on grazing intensity, season of use, and climatic factors. Recovery toward an earlier successional stage would be expected with reduced grazing pressure (Dyksterhuis 1949) unless arid lands are significantly degraded by stress or disturbance (Westoby et al. 1989; Laycock 1991).

Reproductive Density in Relation to Grazing

Stevens et al. (1977) found that both vigor and reproduction of winterfat were reduced in the Steptoe Valley in Nevada by improper season of use, and he recommended no more than 25% utilization during periods of active growth and up to 75% utilization during dormant season use. When protected from grazing, winterfat will reproduce, increasing in both density and foliar cover at some sites and only in foliar cover in others. Rasmussen and Brotherson (1986), in a Utah study on cattle winter range, found significantly greater foliar cover and density of winterfat in areas ungrazed for 26 years versus winter grazed areas. In exclosures protected from grazing for between 5 and 16 years, Rice and Westoby (1978) found that winterfat increased in foliar cover but not in density where it was dominant, and in both foliar cover and density in shadscale-perennial grass communities where it was not dominant.

Biomass in Relation to Grazing

Winterfat response to grazing as measured by aboveground biomass and plant survival varies, and in some cases intensity of grazing determines the impact. Cook and Stoddart (1963) did a clipping study of winterfat at three intensities during four seasons. They concluded that herbage removal during the winter and again in the spring could not exceed 30 percent at any one season without decreasing crown cover and increasing plant mortality. Under light (20%-50% utilization) to heavy (75%

utilization) winter grazing, Chambers and Norton (1993) found higher mortality in non-grazed than grazed plots at Utah's Desert Experimental Range and speculated that changes in plant morphology caused by the pruning effects of winter grazing might actually benefit winterfat by improving its ability to use soil moisture. Other studies suggest alternative results, with winterfat exhibiting increased mortality under a winter grazing scheme when compared to other perennials. In a long term (1935-1968) Utah study of perennial plant survival, West (1979) found that winterfat was the only major perennial with increased mortality due to winter grazing. In a Wyoming winter browsing study of 3-year-old winterfat and fourwing saltbrush (*Atriplex canescens*) plants, Clark and Medcraft (1986) found that 40-50% browsing of winterfat resulted in smaller shrubs compared to no use while saltbrush showed no effect.

Not all studies showed an effect from grazing. Cook and Child (1971) reported that winterfat plants made a 94% recovery of crown cover in 7 years after winter clipping of 90% herbage for 3 years. Hodgkinson (1975), in his eastern Washington study, found that winterfat clipped up to 80% of its aboveground biomass during fall/winter maintained the same levels of growth as unclipped plants.

Seed Viability in Relation to Grazing

Eckert (1954) found that winterfat responded differently depending on the level of winter use. Lightly (35%) clipped plots had the greatest subsequent biomass yield and produced some viable seed. Heavily (95%) clipped plots subsequently produced lower biomass yields but were still able to produce some viable seed.

PROJECT GOAL

The past research suggests that dormant season grazing may impact winterfat's ability to produce levels of biomass achieved by ungrazed plants and to reproduce at levels that maintain stand density. While there is some information on biomass and dormant season grazing (Cook and Stoddart 1963; Clark and Medcraft 1986; Cook and Child 1971; Hodgkinson 1975), there is very little information on grazing's

impact in any season on seed viability (Eckert 1954). To address this gap, this project was designed with the goal of determining the impact of rest from dormant season grazing on winterfat seed viability and aboveground plant biomass. We hypothesized that four years rest from dormant season livestock grazing along with rest from antelope and rabbit browse would result in greater seed viability and aboveground biomass in Catlow Valley winterfat communities.

CHAPTER 2: WINTERFAT SEED VIABILITY AND DORMANT SEASON LIVESTOCK GRAZING

ABSTRACT

Krascheninnikovia lanata (winterfat) is a valuable forage species with an average of 10% crude protein during winter when there are few nutritious options for livestock and wildlife. However, excessive grazing throughout the west has negatively impacted survival of winterfat stands. We hypothesized that four years rest from dormant season livestock grazing, along with rest from antelope and rabbit browse, would result in greater seed viability and aboveground biomass relative to grazed plots.

In locations across the Catlow Valley, Oregon with winterfat communities, two 40 x 40 m plots, a control and an enclosure, were established at each of 15 locations divided among three pastures: north, middle and south. The control plot could be grazed by livestock and wildlife in all seasons (although cattle were only in the study area during the dormant season). The second plot at each location was a large animal enclosure that prevented grazing by cattle and antelope. At four locations a cattle/antelope/rabbit enclosure was also installed. This total of 34 plots was used to test the effects of location and type of use on winterfat seed viability and aboveground plant biomass.

Four years rest from dormant season grazing did not affect the viability of winterfat seed or the levels of aboveground winterfat biomass; however, location across the study area did affect the levels of winterfat aboveground biomass. There was significant variation in the data attributable to unknown factors but represented by the influence that pasture location had on seed state (viable, dead and empty) and winterfat plant biomass. In the most productive locations, increases in winterfat aboveground biomass were correlated with increases in seed viability and decreases in density of winterfat m^2 while increases in winterfat seed viability were correlated with decreases in the percentage of empty seed. In the locations with the highest levels of

dead seed, increases in dead seed were correlated with increases in winterfat density m^2 and decreases in empty winterfat seed.

Plants in the cattle/antelope/rabbit exclosures had the highest winterfat density, the lowest plant biomass, lower levels of empty seed and the highest level of dead seed, the reverse of the most viable plots in the study area. From observation, these plants have a greater amount of woody base growth from prior years and appear more decadent. Further research is needed to see if winterfat seed viability and biomass production is associated with some level of browse. Nuttall's saltbush is the dominant shrub on the site, and its increase is correlated with increases in winterfat aboveground biomass and decreases in the level of dead winterfat seed.

These results suggest that resources which vary by pasture location such as precipitation, soil nutrients, texture, or moisture holding capacity determined levels of winterfat aboveground plant biomass, winterfat seed state, and the density of Nuttall's saltbush and that on high resource sites, winterfat allocates resources to existing plants in rather than creating the new individuals

The lack of response to four years rest from dormant season grazing, the low levels of viable seed, the low density of winterfat, and the encroachment of Nuttall's saltbush all suggest reduced vigor of winterfat in this study area. One possible explanation is that, since recovery toward a later successional stage would be expected with reduced grazing pressure (Dyksterhuis 1949), these arid lands are significantly degraded by stress or disturbance (Westoby et al. 1989; Laycock 1991) and that recovery is no longer possible without significant intervention. This suggests that the study area has crossed an ecological threshold. An alternate possibility is that since recruitment of winterfat is episodic and driven by precipitation events, climatic fluctuations may have prevented the sequence of good precipitation years needed for stand maintaining winterfat recruitment (Pechanec 1964). Further study is needed to evaluate these possibilities.

DESCRIPTION OF THE STUDY AREA

The study was conducted in southeast Oregon, approximately 80 miles south of the town of Burns in a high desert valley described by Mehringer and Wigand (1986) as an historical Pleistocene era lake. The elevation is approximately 1400 meters above sea level (NRCS 2006). The soil is primarily Spangenburg silty clay loam, and there is variation within that soil series across the study area in texture and soil nutrients and pH. Stringham et al. (unpublished data 2002) analyzed samples from 9 soil pits for soil texture and nutrients. They found that of the 9 pits, two had a combination of silt loam or silty clay loam in the A and B horizons, six had a combination of clay loam, clay or loam in the A and B horizons, and one had a combination of clay loam and silty clay loam. Soil % nitrogen by horizon varied from a low of 0.03% to a high of 0.11%. Phosphorus parts per million (ppm) in the A and B horizons varied from a low of 13 to a high of 72. Potassium ppm varied from a low of 385 to a high of 2140. Boron ppm varied from a low of 1.1 to 4.6. Across the study site, pH in the A and B horizons varied from a low of 7.3 to a high of 8.8.

The long-term (1971-2000) average annual temperature and precipitation was 47.8° F (8.7° C) and 12.53 inches (31.8 cm)(OCS 2008). The average maximum and minimum temperatures range from 63.3° F (17.4° C) in the summer to 32.3° F (0.2° C) in the winter. The actual extremes range from 102° F (38.8° C). in August to -27° F (-32.7° C) in December. The average annual precipitation is 12.53 inches (31.8 cm), with much coming in the winter months as snow. In 2005 there was above average precipitation at 16.6 inches (42.2 cm), and in 2004 precipitation was close to average with 11.33 inches (28.8 cm). All the other years from 2001 to 2007 had below average precipitation (see Appendix B for climate graphs).

Since the 1870s, the area has historically been used for livestock grazing (French 1972). Today the valley is grazed by 1500 to 1800 head of English bred cows during the dormant season (November to mid-March) and antelope year round. In addition, feral horses have been sighted in the area; however, significant impact on the

winterfat community by horses has not been documented. The primary small herbivores are blacktailed jackrabbits.

The basin is approximately 30 square miles and consists of three pastures from south to north: 60,000 acres, 20,000 and 24,000 respectively. In 2002, fifteen 40-meter by 40-meter control plots and 19 exclosures were randomly located within the winterfat-dominated plant communities at 15 locations, five locations in each pasture.

Vegetation within the control plots and exclosures was surveyed in 2002 when the plots were established. The densities of the species are shown in the table below (Stringham et al. unpublished data 2002).

Table 1: Vegetation Density m^2 in 2002.

Common Name	Scientific Name	Density m^2
winterfat	<i>Krascheninnikovia lanata</i>	1.90
Nuttall's saltbush	<i>Atriplex nuttallii</i>	3.14
Rabbitbrush	<i>Chrysothamnus viscidiflorus</i>	0.01
Squirreltail	<i>Elymus elemoides</i>	1.29
Indian ricegrass	<i>Achnatherium hymenoides</i>	0.05
Sandberg's bluegrass	<i>Poa secunda</i>	0.17
Creeping wildrye	<i>Leymus triticoides</i>	2.50
cheatgrass	<i>Bromus tectorum</i>	0.96
Clasping leaf pepperweed	<i>Lepidium perfoliatum</i>	2.50
Annual Mustards		0.45
Forbs		1.47

Findings from Matney et al. (unpublished data 2007) indicate that winterfat decreased from 1.90 plants m^2 to 1.80 plants m^2 , and Nuttall's saltbush increased from

3.1 plants m² to 3.6 plants m². In addition, Matney et al. (unpublished data 2007) reported that during the winter of 2006, winterfat plants on the study area were grazed from an average height of 20.5 cm to an average height of 5 cm during the dormant season, an average use of 76%. There was no statistically significant difference between the heights of grazed shrubs from pasture to pasture despite the difference in pasture sizes.

EXPERIMENTAL DESIGN

In a design set up by Stringham et al. (2002), locations across the Catlow Valley with winterfat communities were identified, and 15 were randomly selected for study, five within each pasture. Two 40m x 40 m plots were established at each of the 15 locations, and one was randomly assigned as a control and the other as an exclosure. The control plot was marked but unfenced and could be grazed by livestock and wildlife in all seasons. The second plot at each location was a large animal exclosure that prevented grazing by cattle and antelope. At four locations a cattle/antelope/rabbit exclosure was also installed. Total number of plots equaled 34. Since livestock were only on the study area during the winter, this design created three types of use: (1) control plot (year round wildlife/winter livestock grazing), (2) cattle/antelope exclosure (year round small animal [primarily rabbits] grazing), and (3) cattle/antelope/rabbit exclosure (no grazing).

A two factor completely randomized design was used to test the effects of pasture location and type of use on seed viability and aboveground plant biomass. Location had three levels: north, middle and south pastures. Type of use had three levels: control, cattle/antelope exclosure, and cattle/antelope/rabbit exclosure.

METHODS

Winterfat Aboveground Plant Biomass measurement

In order to determine if aboveground biomass differs between the three treatments, eight randomly selected winterfat plants in each of the 34 plots were

clipped in June 2006 at the peak of the growing season. Plant material was wet weighed, dried for 48 hours at 50°C, and reweighed to determine winterfat aboveground biomass on a dry weight basis.

Winterfat Seed Viability Measurement

In October 2006, seed was gathered by handstripping random plants from each plot to yield approximately 1,000 seeds per plot. A total of 33 plots comprised the sample because one of the control plots had been grazed of all seed. An average of 20 plants per plot were sampled with a range of 4 to 37 plants. Seed from all plants in the plot were combined, and two sets of one hundred seeds per plot were randomly selected from the 1,000+ seed sample and tested for viability at the Oregon State University Seed Lab using the Tetrazolium Test (TZ) (AOSA 2000). The TZ is a biochemical test that differentiates live from dead tissue of seed embryos on the basis of dehydrogenase enzyme activity (respiration enzymes). Filled seeds were classified as viable, dead, or abnormal by distinguishing dead and living cells in the embryo and endosperm tissue. Abnormal seeds were those which had sustained mechanical or thermal damage (AOSA 2000).

DATA ANALYSIS

A two-factor, completely randomized Analysis of Variance (ANOVA) ($\alpha = 0.10$) was used to detect differences among pasture location means for seed viability by type of use and pasture location means for aboveground plant biomass by type use. The analysis was completed using the general linear model (Proc GLM) in SAS (SAS Institute, Cary, NC, U.S.A).

Proc GLM was chosen to perform the Analysis of Variance rather than Proc ANOVA because the unequal number of exclosures created an unbalanced design which was accounted for by Proc GLM's mathematical methods. P-values were taken from the Type III Sums of Squares table rather than the Type I Sums of Squares table, which is also recommended with unbalanced designs because all sources of variance

are evaluated for each variable. All means were obtained using the Least Squares Means statement in SAS, which accounts for the unbalanced design by providing adjusted means (Cody and Smith 1997).

SAS Proc GLM was used to perform an Analysis of Covariance (ANCOVA) to detect differences in nonviable seed related to different levels of biomass, seed viability, or winterfat density accounting for the effect of location. The model used type of nonviable seed (dead, empty, abnormal) as the response variable (dead/empty/abnormal = biomass/viability/density + pasture location).

Linear regression analysis was used to detect relationships between winterfat plant biomass, seed state, and shrub density as well as relationships between Nuttall's saltbush density and winterfat density m^2 and winterfat seed state (normal, abnormal, dead, empty) using Proc REG in SAS. SAS Proc CORR was used to detect underlying correlation between seed states.

RESULTS AND DISCUSSION

Variability in Seed Viability and Aboveground Biomass

Winterfat seed viability was highly variable, ranging between 0.50% and 37.33% with a mean viability of 11.5% across the study area (Table 2). Abnormal seed levels were low and highly variable with a mean of 0.12% abnormal seeds per plot. The minimum value was 0.00% abnormal seed and the maximum value was 0.67% abnormal seed (Table 3). Dead seed levels were highly variable with a mean of 13.3% dead seeds per plot (Table 4). The minimum value was 0.00% dead seeds and the maximum value was 39.3% dead seeds (Table 4). Empty seed levels were relatively consistent with a mean of 75.1% empty seed per plot. The minimum value was 46.2% empty seed and the maximum value was 99.5% empty seed (Table 5).

Table 2: Winterfat Seed Viability Levels for Each Plot. Key:N=north pasture, M=middle pasture, S=south pasture O=Control, X= Excludes cattle/antelope, XB=Excludes cattle/antelope/rabbits.

Plot	% Viability	Plot	% Viability	Plot	% Viability
NC1-O	4.00	MC2-X	14.25	SC1-O	4.83
NC1-X	11.33	MC2-XB	7.00	SC1-X	0.50
NC2-X	9.00	MC3-O	7.67	SC2-O	6.33
NC3-O	8.50	MC3-X	5.00	SC2-X	5.67
NC3-X	21.83	MC3-XB	10.67	SC3-O	17.00
NC4-O	4.67	MC4-O	13.33	SC3-X	7.00
NC4-X	1.50	MC4-X	15.50	SC4-O	20.17
NC4-XB	12.75	MC5-O	17.50	SC4-X	37.33
NC5-O	12.17	MC5-X	34.83	SC4-XB	10.50
NC5-X	5.83	SC0-O	6.67	SC5-O	5.17
MC2-O	10.17	SC0-X	13.50	SC5-X	16.67

Table 3: Winterfat Abnormal Seed Levels for Each Plot. Key: N=north pasture, M=middle pasture, S=south pasture O=Control, X= Excludes cattle/antelope, XB=Excludes cattle/antelope/rabbits.

Plot	% Abnormal	Plot	% Abnormal	Plot	% Abnormal
NC1-O	0	MC2-X	0.50	SC1-O	0
NC1-X	0.17	MC2-XB	0	SC1-X	0
NC2-X	0	MC3-O	0.67	SC2-O	0
NC3-O	0.17	MC3-X	0	SC2-X	0.17
NC3-X	0	MC3-XB	0.50	SC3-O	0.17
NC4-O	0.17	MC4-O	0	SC3-X	0.50
NC4-X	0	MC4-X	0	SC4-O	0.17
NC4-XB	0	MC5-O	0	SC4-X	0.17
NC5-O	0	MC5-X	0	SC4-XB	0
NC5-X	0	SC0-O	0	SC5-O	0
MC2-O	0	SC0-X	0.33	SC5-X	0.17

Table 4: Winterfat Dead Seed Levels for Each Plot. Key: N=north pasture, M=middle pasture, S=south pasture O=Control, X= Excludes cattle/antelope, XB=Excludes cattle/antelope/rabbits.

Plot	% Dead	Plot	% Dead	Plot	% Dead
NC1-O	14.50	MC2-X	26.25	SC1-O	9.75
NC1-X	8.17	MC2-XB	26.50	SC1-X	0.00
NC2-X	6.00	MC3-O	26.33	SC2-O	9.17
NC3-O	28.00	MC3-X	12.83	SC2-X	8.33
NC3-X	11.33	MC3-XB	29.33	SC3-O	10.83
NC4-O	11.33	MC4-O	4.50	SC3-X	10.50
NC4-X	13.50	MC4-X	6.00	SC4-O	8.83
NC4-XB	7.75	MC5-O	4.50	SC4-X	16.33
NC5-O	13.83	MC5-X	4.67	SC4-XB	10.00
NC5-X	11.50	SC0-O	10.67	SC5-O	11.33
MC2-O	39.33	SC0-X	10.33	SC5-X	17.00

Table 5: Winterfat Empty Seed Levels for Each Plot. Key: N=north pasture, M=middle pasture, S=south pasture O=Control, X= Excludes cattle/antelope, XB=Excludes cattle/antelope/rabbits.

Plot	% Empty	Plot	% Empty	Plot	% Empty
NC1-O	81.50	MC2-X	59.00	SC1-O	85.75
NC1-X	80.33	MC2-XB	66.50	SC1-X	99.50
NC2-X	85.00	MC3-O	65.33	SC2-O	84.50
NC3-O	63.33	MC3-X	82.17	SC2-X	85.83
NC3-X	66.83	MC3-XB	59.50	SC3-O	72.00
NC4-O	83.83	MC4-O	82.17	SC3-X	82.00
NC4-X	85.00	MC4-X	78.50	SC4-O	70.83
NC4-XB	79.50	MC5-O	78.00	SC4-X	46.17
NC5-O	74.00	MC5-X	60.50	SC4-XB	79.50
NC5-X	82.67	SC0-O	82.67	SC5-O	83.50
MC2-O	50.50	SC0-X	75.83	SC5-X	66.17

Aboveground biomass levels were also highly variable with a mean of 19.47 grams per plant. The minimum value was 6.48 grams and the maximum value was 60.73 grams (Table 6).

Table 6: Winterfat Biomass (g) Levels for Each Plot. Key: N=north pasture, M=middle pasture, S=south pasture O=Control, X= Excludes cattle/antelope, XB=Excludes cattle/antelope/rabbits.

Plot	Biomasss (g)	Plot	Biomasss (g)	Plot	Biomasss (g)
NC1-O	8.25	MC2-X	9.96	SC1-O	8.21
NC1-X	13.30	MC2-XB	9.56	SC1-X	9.00
NC2-O	6.48	MC3-O	22.84	SC2-O	24.11
NC2-X	9.28	MC3-X	21.98	SC2-X	16.14
NC3-O	38.21	MC3-XB	17.54	SC3-O	10.64
NC3-X	25.60	MC4-O	30.94	SC3-X	14.73
NC4-O	13.28	MC4-X	60.73	SC4-O	18.36
NC4-X	11.59	MC5-O	55.31	SC4-X	12.03
NC4-XB	17.29	MC5-X	46.84	SC4-XB	16.34
NC5-O	15.19	SC0-O	16.36	SC5-O	17.36
NC5-X	12.99	SC0-X	13.25	SC5-X	31.13
MC2-O	7.21				

Many factors that were outside the scope of this study could have been responsible for variation of winterfat seed viability and biomass production across the landscape. Although all plots are on the same soil series, there is soil texture variation identified by Stringham et al. (2002), which can result in varying infiltration rates (Gates et al. 1956) and different water holding capacity across the study area (Sala et al. 1988). Winterfat seed vigor could have been influenced by soil texture or clay content as it has been on other sites. Coffin and Lauenroth (1992) found that soil texture (coarse or fine) and clay content influenced the number of seeds produced by *Bouteloua gracilis*. Winterfat seed vigor could also have been influenced by differing levels of soil nutrients which also vary across the study area (Stringham et al. 2002). Goodman (1973) found that soil nutrients and salinity affected the growth of winterfat, which decreased with increased salt and boron, and Nuttall's saltbush, which increased with increased salt and boron. Winterfat biomass levels could have been affected by inherent spatial variability in precipitation or differences due to differences in the terrain. Variability in snow distribution due to the direction and amount of wind

during snowfall could have affected soil moisture recharge as it has on other sites (West and Caldwell 1983).

Winterfat seed viability levels could have been affected by variations in hydrology. In a study of another arid system shrub, mountain big sagebrush (*Artemisia tridentata* Nutt. ssp. *Vaseyana*), Spaeth et al. (2007) found that the vegetation, plant composition, and soil physical properties varied with the hydrology of microsites (shrub coppice, shrub dripline, and varying distances along the interspace). Soil water holding capacity could have had an impact on winterfat seed viability or winterfat aboveground plant biomass. Although there are no similar studies for winterfat, Sala et al. (1988) found that two variables, annual precipitation and soil water holding capacity, accounted for the variability in production at their central grassland site. Spring and summer precipitation patterns across the Catlow Valley may vary significantly. In order to determine if precipitation during winterfat vegetative and reproductive growth is critical, precipitation would need to be measured at each plot.

We observed some wind erosion in the study area, and researchers looking at the impact of wind erosion on a bladder saltbush (*Atriplex vesicaria*) site described the movement of the topsoil to the point where the site became an unvegetated claypan (Westoby et al. 1989).

Factors such as differences in hydrology, soil texture and clay content, water holding capacity and salinity could have caused variation in winterfat's ability to access moisture needed for biomass production and development of viable seed. Differences in nutrient levels, salinity and degree of erosion could have provided competitive advantages to other plants, limiting resources winterfat needed for biomass production and development of viable seed. For example, Nuttall's saltbush, which has greater average density across the study area than winterfat, has replaced climax communities on other sites where erosion occurred in the top three soil horizons (West and Ibrahim 1968). Soil trampling during the winter grazing period has been observed in the study area, particularly in wetter areas. Winter grazing could have created compaction layers in some areas, limiting winterfat's ability to grow a

deep taproot to access water needed for biomass production and development of viable seed. An additional possibility is that altered soil aggregate stability has prevented deep water infiltration resulting in roots close to the surface because there is no deep water.

Factors Related to Viability

The Effect of Dormant Season Grazing on Winterfat seed Viability

Analysis of variance was used to determine if seed viability was different across the three types of use: (1) control plot (year-round wildlife grazing/winter livestock grazing), (2) cattle/antelope enclosure (year-round small animal grazing), and (3) cattle/antelope/rabbit enclosure (no grazing and by location [north, middle and south pasture]). Results indicated no difference in mean seed viability levels for all types of use and locations (Table 7). Four years rest from dormant season livestock grazing along with rest from antelope and rabbit browse did not affect the viability of winterfat seed either by type of use ($p=0.5209$) or by location ($p=0.4459$).

Table 7: The Means \pm Standard Error for Winterfat Seed Viability by Type of Use and Pasture Location. Means were not significantly different.

Factor	Mean % Seed Viability \pm SE
Type of Use	
Control Plot	9.85 \pm 2.24
Cattle/Antelope Enclosure	13.46 \pm 2.17
Cattle/Antelope/Rabbit Enclosure	9.65 \pm 4.21
Location	
North Pasture	8.51 \pm 2.85
Middle Pasture	13.32 \pm 2.71
South Pasture	11.13 \pm 2.59

There are a number of possible explanations for the lack of response to grazing. The variability in other factors such as soil nutrients, texture, or moisture holding capacity (Coffin and Lauenroth 1992; Sala et al. 1988; Goodman 1973) across

the study area may have masked the effects of grazing. It may be necessary to collect seed samples over a longer time period or earlier in the dispersal phase rather than at the end of seed dispersal. Four years of rest from dormant season livestock grazing may not have been long enough to detect any change in winterfat seed viability due to factors such as climatic fluctuations. Additional years of seed viability tests or increased sample size may be needed to confirm the results of this study, but other factors studied may provide some insight into the patterns of winterfat seed viability, particularly the relationship of winterfat seed viability and winterfat aboveground plant biomass.

The Relationship between Winterfat Seed Viability and Winterfat Aboveground Plant Biomass

Regression analysis suggests that there is a positive relationship between winterfat aboveground plant biomass and winterfat seed viability ($p=0.0262$, $R^2=0.1495$, slope= 0.24). The seed produced by winterfat plants with greater biomass had a higher percentage of viability. The relative production of biomass is a measure of the plant's success in energy, nutrient and moisture capture (Ewel 1987), which are all resources required to produce viable seed.

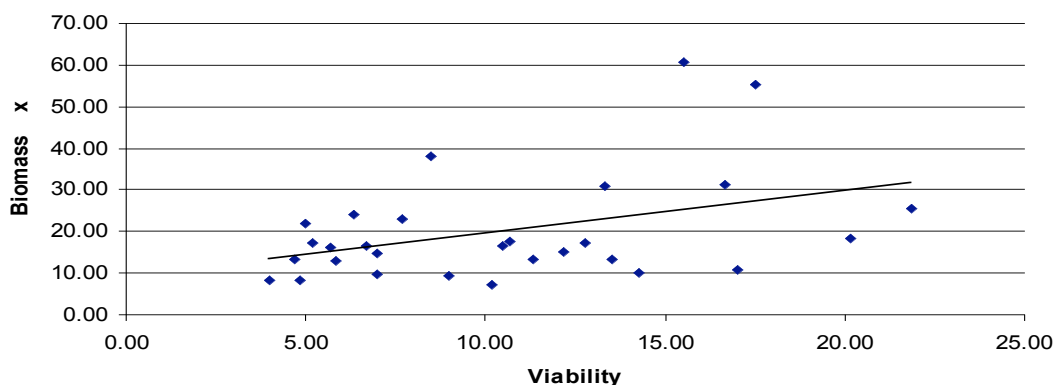


Figure 1: Winterfat Biomass and Winterfat Seed Viability Regression Plot

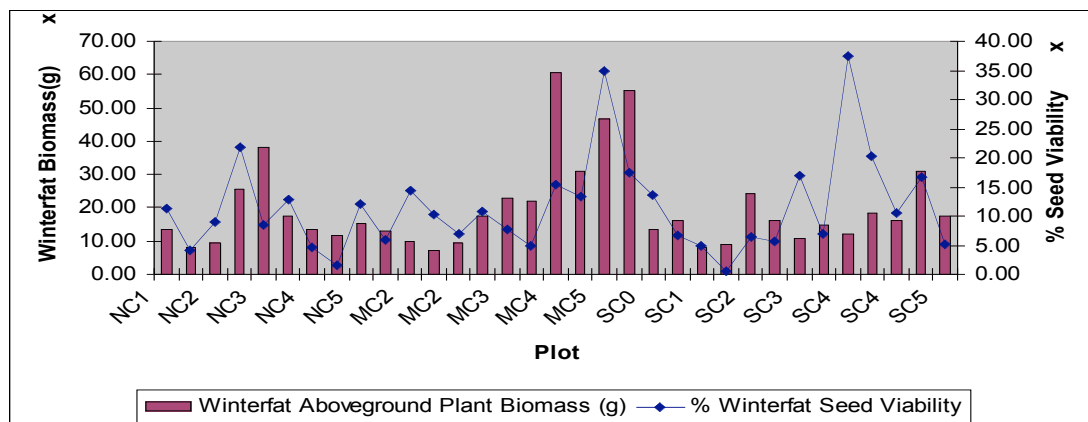


Figure 2: Winterfat Biomass and Winterfat Seed Viability by Plot. Key: N=north pasture, M=middle pasture, S=south pasture.

Seed viability is a product of the environmental conditions during seed formation and of physiological characteristics of the seed (Woodmansee 1971). Maternal resource allocation to reproduction is typically less than 30% of net primary production, reflecting the plant's strategy in the face of environmental stress and plant competition. A seed contains the embryo and food reserves whose quality is determined by the mother plant's allocation of carbon and nutrients to reproduction. This allocation varies depending on environmental conditions during seed formation (Lambers et al. 1998). Winterfat biomass production is greatest when it has access to high levels of moisture (Kinsinger and Strickler 1961). This suggests that the conditions that support higher biomass growth, particularly moisture capture, also support higher seed viability and that larger plants have the site resources to produce more viable seed. Pasture location affected the level of biomass production, and it is possible that levels of nutrients, differential patterns of precipitation, and/or soil water holding capacity vary across pasture locations in ways that support differential biomass growth with larger plants with more resources producing more viable seed.

Viable seed is one of four possible states identified for winterfat seed from the study area, and an understanding of the factors affecting non-viable seed may help explain the results. To gain an understanding of the underlying relationships between

the seed state of viable and non-viable seed, correlation analysis was performed on the data from winterfat seed testing.

Viable vs. Nonviable Seed

Underlying Relationships between Viable, Dead, and Empty Seed

Correlation analysis shows that the percentage of viable winterfat seed is negatively correlated to the percentage of empty winterfat seed (correlation coefficient=-0.66, $p=0.0001$) but not to the percentage of dead winterfat seed. The percentage of empty winterfat seed and the percentage of dead winterfat seed are negatively correlated (correlation coefficient =-0.70, $p= 0.0001$).

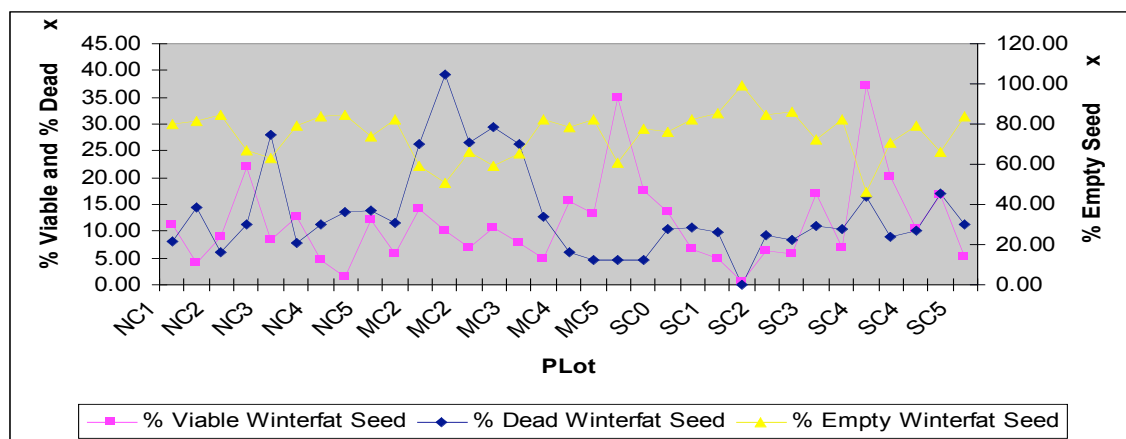


Figure 3: Winterfat Percentage of Viable, Dead, and Empty Seed by Plot. Key: N=north pasture, M=middle pasture, S=south pasture.

Winterfat viable seed and winterfat aboveground biomass are significantly positively related (Figures 1 and 2), and empty winterfat seed and viable winterfat seed are significantly negatively correlated (Figures 1 and 2). Stephenson (1981) characterizes the plant's decision to abort a seed rather than invest the carbon and nutrients to bring it to maturity as a way of matching fruit production to site resources. This suggests that on sites with the resources to produce higher levels of winterfat aboveground biomass, winterfat plants can effectively allocate those resources to the

creation of viable seed and effectively abort the seed they cannot support. Spring and summer precipitation patterns across the Catlow Valley may vary significantly. In order to determine if precipitation during plant growth and seed development is critical, precipitation would need to be measured at each plot. To identify other factors in the study area influencing the levels of empty seed, analysis of covariance was performed by pasture location and type of use.

Factors Affecting the Percentage of Empty Seed

Analysis of covariance indicated that the percentage of empty seed was affected by pasture location interacting with biomass ($p=0.0279$). This is consistent with the finding (Table 8) that there was a significant pasture location effect on biomass.

As mentioned above, differences in hydrology, soil texture and clay content, water holding capacity, and salinity across pasture locations can represent variation in site resources available to the plant. Allocation to reproduction typically represents from 1% to 30% of the allocation to net primary production (Lambers et al. 1998), representing the plant's strategy in the face of stress and disturbance. The analysis of winterfat aboveground biomass by pasture location (Table 8) showed that pasture location affects winterfat aboveground biomass, and this supports an interpretation that variations in resources between pasture locations determine the allocation winterfat makes to vegetative production at the expense of seed production.

The other primary form of non-viable winterfat seed in the study, dead seed was negatively correlated with empty seed, and it, too, was influenced by pasture location in combination with other factors, the level of viable seed, the degree of winterfat plant density m^2 , and the level of winterfat aboveground biomass.

Factors Affecting the Percentage of Dead Winterfat Seed

Analysis of covariance shows that the interaction of pasture location and percent winterfat seed viability ($p=0.0258$), the interaction of pasture location and winterfat biomass ($p= <.0001$), and the interaction of pasture location and winterfat density m^2 ($p=0.0574$) all affect the percentage of dead winterfat seed. While there is

no correlation between dead seed and viable seed, dead seed was affected by the interaction of viable seed and pasture location. Dead seed, like empty seed, was affected by the interaction of biomass and pasture location. Unlike viable seed or empty seed, dead seed was also affected by the density of winterfat m^2 in interaction with pasture location.

Regression analysis showed that the relationship of the percentage of dead winterfat seed with the density of Nuttall's saltbush m^2 was significant, inverse, and not linear ($p= 0.0228$, $R^2= 0.1563$, slope= -1.28). In plots where the percentage of dead seed was lower, Nuttall's saltbush density was higher.

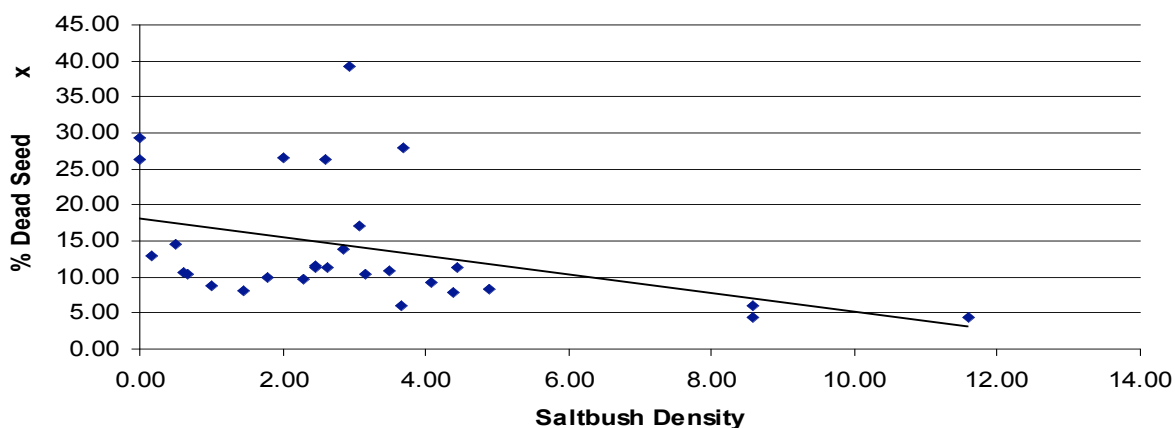


Figure 4: Saltbush Density m^2 and Percent Dead Seed Regression Plot

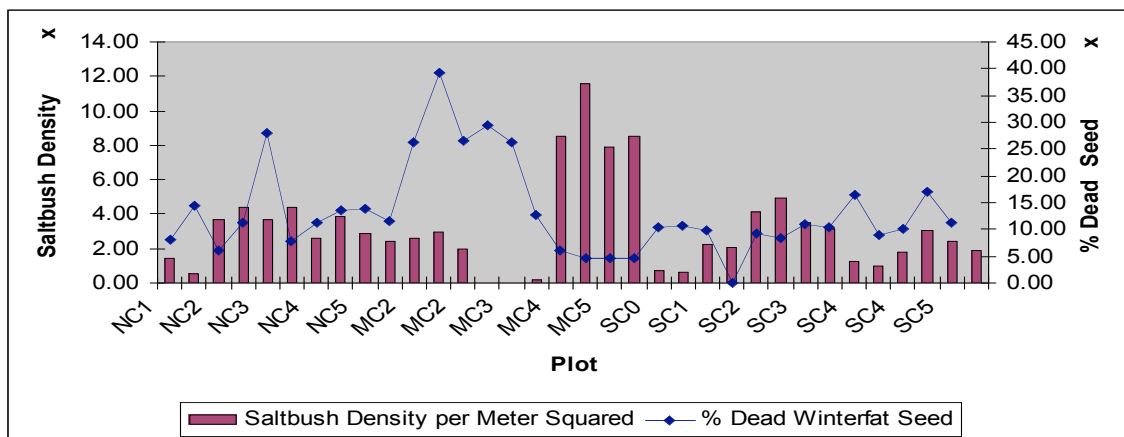


Figure 5: Saltbush Density m^2 and Percent Dead Seed by Plot. Key: N=north pasture, M=middle pasture, S=south pasture.

The data from Stringham et al. (2002) and Matney (2007) indicate an overall trend in the study area of an increase in density of Nuttall's saltbush. Plots with less saltbush density may represent areas where resources are not sufficient to support saltbush expansion on par with the rest of the study area or resources are not sufficient to make the site the first area of expansion. This would be consistent with an interpretation that increases in dead winterfat seed are caused by factors in the study area that are not conducive to the vigor of either species.

Factors Related to Biomass

The Effect of Dormant Season Grazing on Winterfat Aboveground Plant Biomass

Analysis of variance (Table 8) showed that differences in the type of use did not affect the amount of aboveground biomass produced by winterfat plants ($p=0.7470$). Pasture location was significantly related to the amount of aboveground plant biomass produced by winterfat plants ($p=0.0297$), suggesting that factors which vary across the study area such as soil nutrients and texture (Stringham et al. 2002) and the resulting differences in infiltration and moisture holding capacity (Gates et al.

1956; Coffin and Lauenroth 1992; Sala et al. 1988; Goodman 1973) determined levels of winterfat aboveground annual biomass.

Table 8: The Means and Standard Errors for Aboveground Plant Biomass (g) by Type of Use and Location. Means by type of use were not significantly different. Location means that were not significantly different are indicated with a matching letter (a).

Factor	Mean Plant Biomass (g) \pm SE
Type of Use	
Control Plot	20.40 \pm 3.24
Cattle/Antelope Exclosure	21.46 \pm 3.24
Cattle/Antelope/Rabbit Exclosure	12.94 \pm 6.29
Location	
North Pasture	13.65 \pm 4.10 ^a
Middle Pasture	27.23 \pm 4.10
South Pasture	13.93 \pm 3.87 ^a

As was the case in some other dormant season grazing studies (Cook and Child 1971; Hodgkinson 1975), analysis indicates that rest from dormant season grazing, in this case for 4 years, had no effect on winterfat aboveground biomass (Table 8). However, the underlying large variation in winterfat aboveground biomass across the valley (Table 6) may be masking grazing effects. Additional years of winterfat biomass sampling or increased sample size may be needed to confirm the results of this study.

There was a significant effect on winterfat aboveground biomass by pasture location (Table 8), and in an attempt to understand the impact of other factors studied, correlation analysis was performed to better understand the underlying relationships between biomass and shrub density.

Underlying Relationships between Winterfat Aboveground Biomass and Shrub Density

Correlation analysis showed that the density m^2 of winterfat and Nuttall's saltbush are negatively correlated ($r = -0.66$, $p = 0.0001$) with each other. Winterfat density m^2 is negatively correlated with winterfat aboveground plant biomass ($r = -0.37$, $p = 0.0321$). Saltbush density m^2 was positively correlated with winterfat aboveground plant biomass ($r = 0.68$, $p = 0.0001$).

As winterfat aboveground biomass increased, winterfat density decreased. At the same time, as winterfat density m^2 decreased, saltbush density m^2 increased.

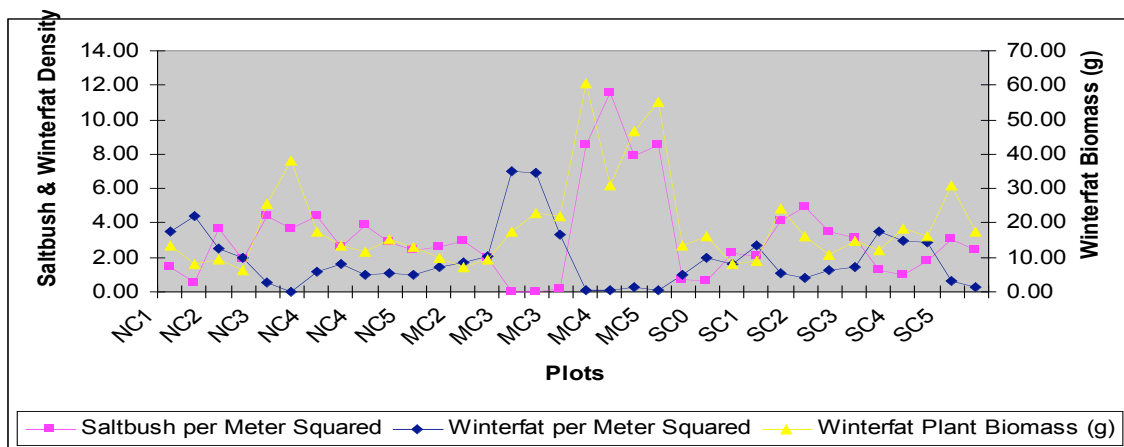


Figure 6: Biomass, Saltbush, and Winterfat Density m^2 by Plot. Key: N=north pasture, M=middle pasture, S=south pasture.

Aboveground Biomass and the Densities of Winterfat and Nuttall's Saltbush

Winterfat biomass was affected by the interaction of winterfat density and saltbush density ($p = 0.0001$).

Correlation analysis (Figure 6) showed that as winterfat aboveground plant biomass increased, the density m^2 of winterfat decreased and the density of Nuttall's saltbush m^2 increased. As mentioned above (Figures 1 and 2), winterfat seed viability also increased. Winterfat will forego seed production if environmental conditions are

not sufficient to support growth and reproduction (Stevens 1977; Pechanec 1964). Rice and Westoby (1978) found that winterfat protected from grazing increased in cover but not in density, suggesting that winterfat, as a long lived plant, allocates resources to existing plants rather than the creation of new individuals. It is possible that the increasing density of Nuttall's saltbush is the factor that is preventing winterfat from creating new individuals on a site that has the resources to support both greater winterfat biomass and greater winterfat seed viability.

Nuttall's saltbush is a more competitive plant than winterfat in carbohydrate reserves (Coyne and Cook 1970) and tolerance for erosion (West and Ibrahim 1968) and unlike winterfat is not preferentially grazed by cattle (Turner 1971). Nuttall's saltbush has been increasing in the study area from a density m^2 of 3.2 in 2002 to 3.6 in 2007. At the same time, winterfat has been decreasing from 1.9 plants m^2 in 2002 to 1.8 plants m^2 in 2007. Nuttall's saltbush increase is more extreme in the control plots which are grazed by both livestock (dormant season) and wildlife (year-round).

Table 9: Mean Density of Nuttall's Saltbush by Type of Use, Control Plot, Cattle/Antelope Exclosures, or Cattle/Antelope/Rabbit Exclosures.

Year	All Plots	Control Plots	Cattle/antelope Exclosure	Cattle/antelope /rabbit Exclosure
Saltbush plants m^2 (2002)	3.2	3.2	3.3	2.0
Saltbush plants m^2 (2007)	3.6	4.4	3.2	1.7

Nuttall's saltbush density in the control plots in 2002 was the same as the average across the study area at 3.2 plants m^2 (Stringham et al. 2002) but increased to 4.4 plants m^2 in 2007 while the saltbush average across the study area was 3.6 plants m^2 (Matney 2007).

It is possible that winterfat aboveground biomass and seed viability (Figures 1 and 2) are greater in some plots for the same reason that Nuttall's saltbush density is

greater: some plots have more abundant site resources. Or these phenomena may be related to separate factors that have not been studied.

Observations from Cattle/Antelope/Rabbit Enclosures

While not statistically significant, there were trends in winterfat seed state (viable, abnormal, dead, or empty), winterfat aboveground biomass, and winterfat and Nuttall's saltbush plant density observed in the four cattle/antelope/rabbit enclosures that merit further evaluation. The table of means (Table 10) below shows the relative ranking of the control plot, cattle/antelope enclosures and cattle/antelope/rabbit enclosures by these metrics.

Table 10: Means for Each Metric by Type of Use, Control Plot, Cattle/Antelope Enclosures, or Cattle/Antelope/Rabbit Enclosures.

Metric	All Plots	Control Plots	Cattle/antelope Enclosure	Cattle/antelope /rabbit Enclosure
% Viable Seed	11.50	9.85	13.46	9.65
Biomass (g per plant)	19.47	20.40	21.46	12.94
Winterfat plants m ² (2002)	1.9	1.8	1.6	3.3
Winterfat plants m ² (2007)	1.8	1.8	1.5	3.2
% Abnormal Seed	0.12	0.10	0.13	0.13
% Dead Seed	13.31	14.49	10.84	18.40
% Empty Seed	75.10	75.57	75.70	71.25
Saltbush plants m ² (2002)	3.2	3.2	3.3	2.0
Saltbush plants m ² (2007)	3.6	4.4	3.2	1.7

The most viable locations on this study area are characterized by low winterfat density, high levels of biomass, high levels of empty seed, and low percentages of dead seed (Figures 2 and 4). Plants in the cattle/antelope/rabbit exclosures have the highest winterfat density, the lowest plant biomass, lower levels of empty seed, and the highest level of dead seed. From observation, these plants retained the woody stems from the prior year growth period and appear more decadent. These results suggest that this study area is similar to Utah's Desert Experimental Range where higher levels of winterfat plant mortality were found in ungrazed plots (Chambers and Norton 1993). Further investigation of this observation is warranted.

Summary of Results

We hypothesized that four years rest from dormant season livestock grazing, along with rest from antelope and rabbit browse, would result in greater seed viability and aboveground biomass in protected plots in Catlow Valley winterfat communities relative to grazed plots. However, four years rest was not significant in determining viability of winterfat seed or the levels of aboveground winterfat biomass (Table 7, Table 8).

Location across the study area did affect the level of aboveground winterfat biomass (Figure 8), and there was a significant relationship between the level of aboveground winterfat biomass and winterfat seed viability (Figures 1 and 2). As winterfat aboveground biomass increased, winterfat seed viability increased (Figures 1 and 2).

Winterfat seed viability was inversely correlated with empty winterfat seed (Figure 3), and empty winterfat seed was inversely correlated with dead winterfat seed (Figure 3). As viable winterfat seed increased, empty winterfat seed decreased, and as empty winterfat seed decreased, dead winterfat seed increased (Figure 3).

Location across the study area not only had an effect on winterfat aboveground biomass (which had an effect on viability) (Figure 8), in interaction with other factors, it affected the levels of empty and dead winterfat seed (Figure 3). The percentages of

empty or dead winterfat seed were affected by pasture location interacting with winterfat biomass, and the interaction of pasture location and winterfat seed viability affected the levels of dead winterfat seed. While the interaction term prevents drawing conclusions about what the specific effect of location was on empty and dead winterfat seed, it underscores the importance of location on the ultimate condition of the seed (viable, dead, or empty).

Winterfat seed state (viable, dead, or empty) and winterfat aboveground biomass levels were affected by winterfat density m^2 and Nuttall's saltbush density m^2 (Figures 6, 7 and 8), as well as pasture location. Pasture location and winterfat density m^2 affected the percentage of dead winterfat seed, and the percentage of dead winterfat seed was higher in plots where the density of Nuttall's saltbush was lower (Figures 4 and 5). As winterfat aboveground biomass increased winterfat, seed viability increased, and winterfat density m^2 decreased and Nuttall's saltbush density m^2 increased (Figures 6, 7 and 8). As winterfat density m^2 decreased, saltbush density m^2 increased (Figure 4).

Taken together, these results show the following tendencies: viable winterfat seed, winterfat aboveground biomass, and density of Nuttall's saltbush increase as winterfat density decreases; dead winterfat seed and winterfat density increase as empty winterfat seed and the density of Nuttall's saltbush decrease. This suggests that resources which vary by pasture location, such as precipitation, soil nutrients, texture, or moisture holding capacity, may be the environmental drivers in the determination of levels of winterfat aboveground plant biomass, winterfat seed state, and the density of Nuttall's saltbush. Additionally, while not statistically significant, other results suggesting lowered vigor observed in the 4 cattle/antelope/rabbit exclosures merit further evaluation (Table 9).

CHAPTER 3: CONCLUSION

There was considerable variation in the data attributable to unknown factors but influenced by the effect that location had on seed state and winterfat plant biomass.

Vegetation response to changes in dormant season grazing has been highly variable at other sites, and the lack of response in the Catlow Valley is consistent with other work. The most viable locations in this study area are characterized by low winterfat density, high levels of biomass, high levels of empty seed, and low percentages of dead seed. They are also characterized by high Nuttall's saltbush density, indicating that at current saltbush density levels, mature winterfat can still secure site resources; however, recruitment for maintenance of the community was not apparent.

Nuttall's saltbush is a more competitive plant than winterfat in carbohydrate reserves and tolerance for erosion. The density of Nuttall's saltbush has increased since 2002 while at the same time the density of winterfat has decreased. If this trend continues, the winterfat community in the Catlow Valley may be replaced by Nuttall's saltbush.

The winterfat empty seed percentage of 75.1% was high in this study area relative to other locations reported in the literature. It correlates with the percentage of viable seed and the percentage of dead seed, suggesting that the plant attempts to create 25% live seed and resource levels permit less than half that seed to live.

Plants in the cattle/antelope/rabbit exclosures had the highest winterfat density, the lowest plant biomass, lower levels of empty seed, and the highest level of dead seed, the reverse of the most viable plots in the study area. From observation, these plants had a greater amount of retained woody stems from prior years and appear more decadent. Further research is needed to determine if winterfat seed viability and biomass production is associated with some level of browse.

The lack of response to rest from grazing, the high levels of empty and dead seed, the low density of winterfat, and the encroachment of Nuttall's saltbush all suggest reduced vigor of winterfat in this study area. One possible explanation is that, since recovery toward a later successional stage would be expected with reduced grazing pressure (Dyksterhuis 1949), these arid lands are so significantly degraded by stress or disturbance (Westoby et al. 1989; Laycock 1991) that recovery is no longer possible without significant intervention. This suggests that the study area has crossed an ecological threshold. An alternate possibility is that since recruitment of winterfat is episodic and driven by precipitation events, climatic fluctuations have prevented the sequence of good precipitation years necessary for stand maintaining winterfat recruitment (Pechanec 1964). Further study is needed to evaluate these possibilities.

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APPENDICES

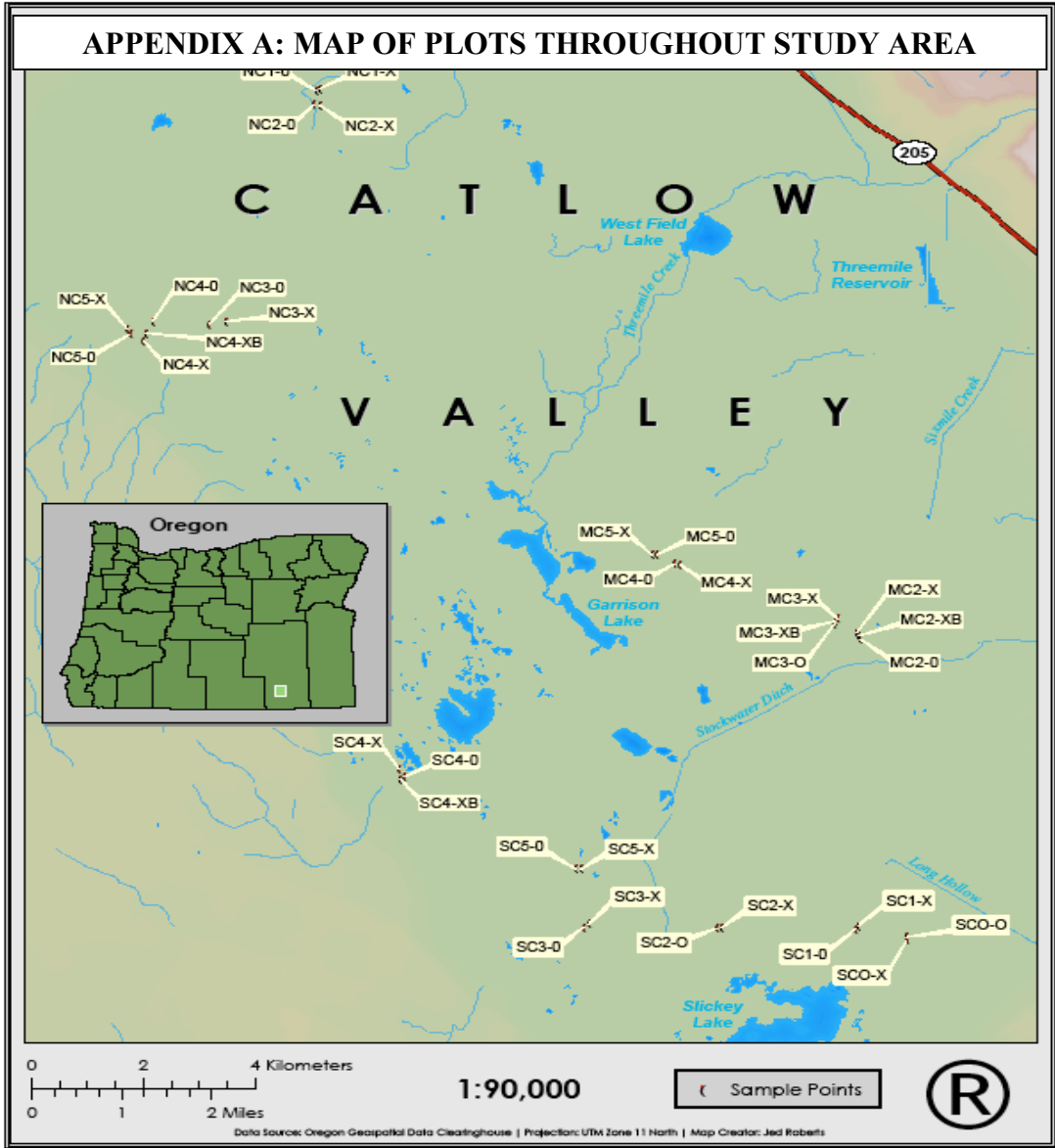


Figure A.1: Map of Plots throughout Study Area.

APPENDIX B: CLIMATE CHARTS FOR P-RANCH REFUGE NEAR THE STUDY AREA

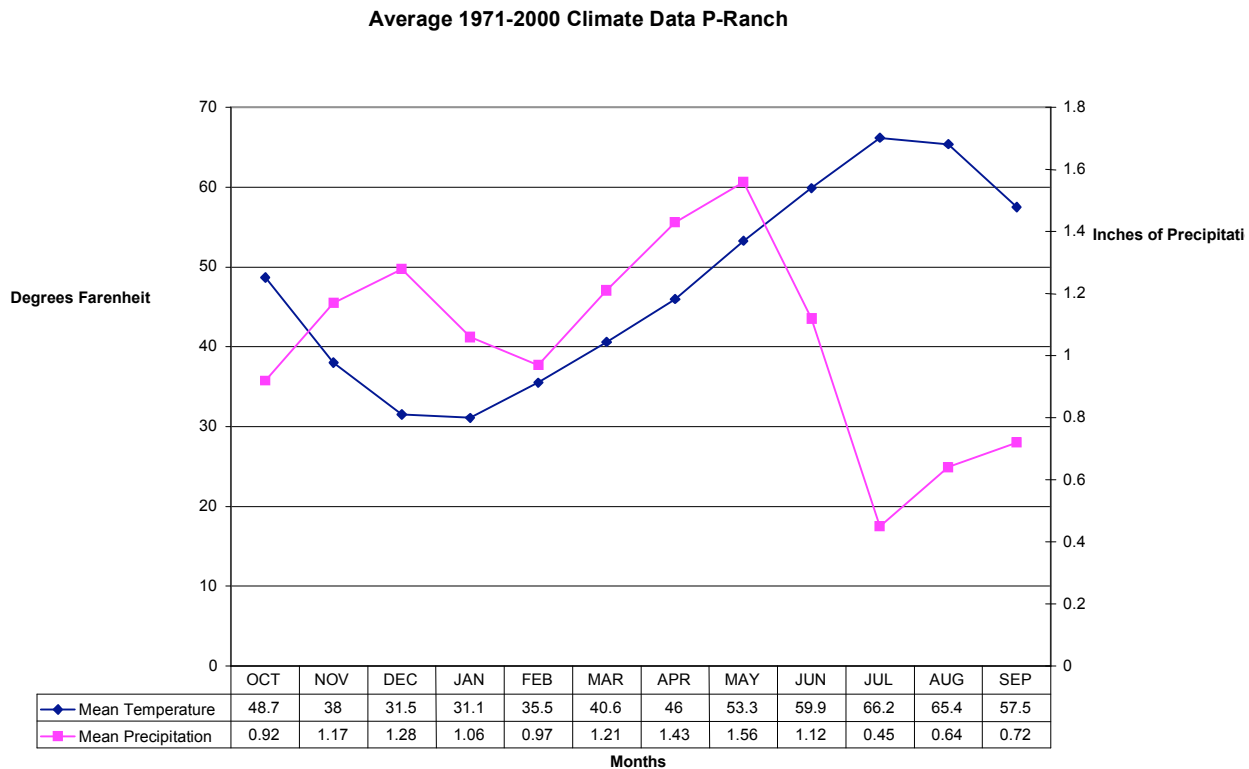


Figure B.1: Average Temperature and Precipitation for the P-Ranch Refuge Weather Station from 1971 to 2000.

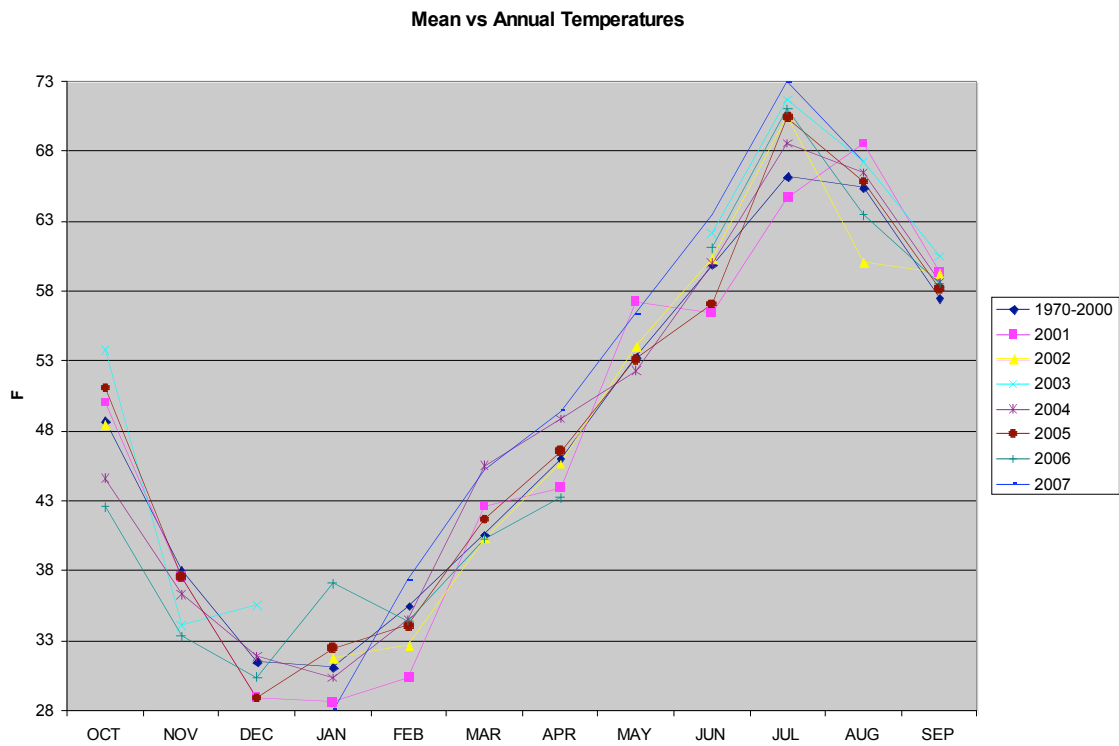


Figure B.2: Thirty-year Average Annual Temperature Versus Average Temperatures From 2001 to 2007.

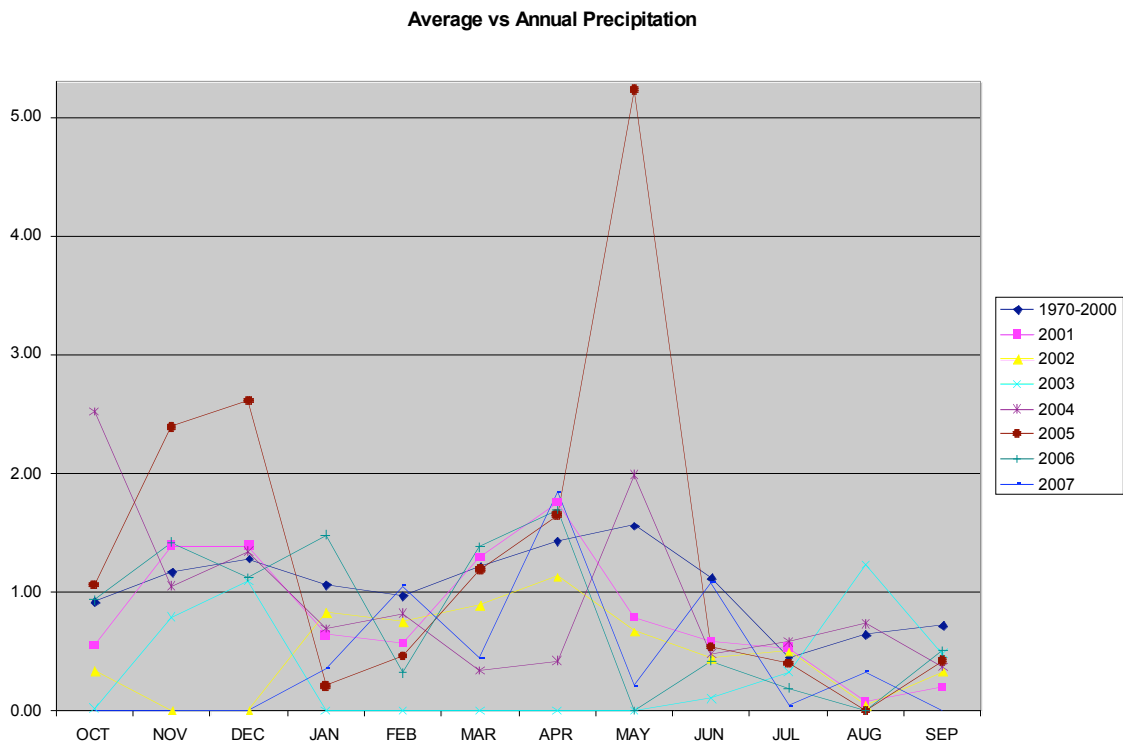


Figure B.3: Thirty-year Average Precipitation Versus Average Precipitation for the Years 2001 to 2007.

APPENDIX C: ANALYSIS OF VARIANCE TABLES

Test: Effect of Type of Use and Pasture Location on Winterfat Seed Viability

ANOVA Table Proc GLM

Dependent variable: Winterfat Seed Viability

Source	Degrees of Freedom
Type of Use	2
Pasture	2
Residual	28

Type 3 Tests of Effects

Effect	Numerator DF	Denominator DF
Type of Use	2	28
Pasture	2	28

Figure C.1: ANOVA of the Effect of Type of Use and Pasture Location on Winterfat Seed Viability.

Test: Effect of Type of Use and Pasture Location on Winterfat Aboveground Biomass

ANOVA Table Proc GLM

Dependent variable: Winterfat Aboveground Biomass

Source	Degrees of Freedom
Type of Use	2
Pasture	2
Residual	28

Type 3 Tests of Effects

Effect	Numerator DF	Denominator DF
Type of Use	2	28
Pasture	2	28

Figure C.2: ANOVA of the Effect of Type of Use and Pasture Location on Winterfat Aboveground Biomass.

Test: Effect of Biomass and Pasture Location on Winterfat % Empty Seed

ANCOVA Table Proc GLM

Dependent variable: Winterfat Aboveground Biomass

Source	Degrees of Freedom
Biomass	1
Pasture	2
Biomass*Pasture	2
Residual	27

Type 3 Tests of Effects

Effect	Numerator DF	Denominator DF
Biomass	1	27
Pasture	2	27
Biomass*Pasture	2	27

Figure C.3: ANCOVA of the Effect of Biomass and Pasture Location on Winterfat Percentage of Empty Seed

Test: Effect of Winterfat Density and Pasture Location on Winterfat % Dead Seed

ANCOVA Table Proc GLM

Dependent variable: Winterfat Density per m2

Source	Degrees of Freedom
Winterfat Density	1
Pasture	2
Density*Pasture	2
Residual	27

Type 3 Tests of Effects

Effect	Numerator DF	Denominator DF
Winterfat Density	1	27
Pasture	2	27
Density*Pasture	2	27

Figure C.4: ANCOVA of the Effect of Winterfat Density and Pasture Location on Winterfat Percentage of Dead Seed

APPENDIX D: ANALYSES PERFORMED

Key: Viability= % Viable Seed, Trt= control, cattle/antelope exclosure, cattle/antelope/rabbit exclosure, Pasture= pasture location, Biomass= winterfat aboveground biomass, KRLA= density m^2 of winterfat, ATNU= density m^2 of Nuttall's saltbush, Dead= % of dead winterfat seeds, Empty=% of empty winterfat seeds, “|” indicates that the interaction was tested and both main effects were tested

Viability Models Tested

Viability =Trt|Pasture
 Viability =Trt Pasture
 Viability =Trt
 Viability= Pasture
 Viability=Biomass|Pasture
 Viability=Biomass
 Viability=Biomass|KRLA
 Viability=Biomass|ATNU
 Viability = KRLA|Pasture
 Viability= ATNU|Pasture
 Viability=ATNU|KRLA
 Viability=ATNU
 Viability= Dead
 Viability= Empty

Biomass Models Tested

Biomass =Trt|Pasture
 Biomass =Trt Pasture
 Biomass =Trt
 Biomass =Viability|Pasture
 Biomass= KRLA|Pasture
 Biomass= ATNU|Pasture
 Biomass=ATNU|KRLA
 Biomass=ATNU
 Biomass= KRLA

Winterfat Density Models Tested

KRLA =Trt|Pasture
 KRLA = Biomass|Pasture
 KRLA = Biomass|ATNU
 KRLA =Trt
 KRLA =Viability|Pasture
 KRLA= ATNU|Pasture
 KRLA=ATNU

Nuttall's saltbush Density Models Tested

ATNU =Trt|Pasture
 ATNU = Biomass|Pasture
 ATNU = Biomass|KRLA
 ATNU = Biomass
 ATNU =Trt
 ATNU =Viability|Pasture
 ATNU= KRLA|Pasture
 ATNU=KRLA

Dead Seed Models Tested

Dead =Trt|Pasture
 Dead =Trt
 Dead=Viability|Pasture
 Dead=Biomass|Pasture
 Dead=Biomass|ATNU
 Dead = KRLA|Pasture
 Dead= ATNU|Pasture
 Dead=ATNU|KRLA
 Dead=ATNU

Empty Seed Models Tested

Empty =Trt|Pasture
 Empty =Trt
 Empty=Viability|Pasture
 Empty=Biomass|Pasture
 Empty=Biomass|ATNU
 Empty=Biomass|KRLA
 Empty = KRLA|Pasture
 Empty= ATNU|Pasture