Climatic influences on sagebrush establishment in Arid Rangelands: Applications for rangeland rehabilitation.

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Animal Science

by

Erin V. Hourihan

Dr. Barry L. Perryman/Thesis Advisor

December, 2011
We recommend that the thesis
prepared under our supervision by

ERIN V. HOURIHAN

entitled
Climatic influences on sagebrush establishment in Arid Rangelands: Applications for rangeland rehabilitation.

be accepted in partial fulfillment of the
requirements for the degree of

MASTER OF SCIENCE

Barry L. Perryman, Ph.D., Advisor

L. Ben Bruce, Ph.D., Committee Member

Elizabeth A. Leger, Ph. D., Graduate School Representative

Marsha H. Read, Ph. D., Dean, Graduate School

December, 2011
Abstract
Sagebrush-dominated ecosystems are threatened by altered fire regimes, invasive species, infrastructure development, conversion to cropland, and encroachment by woody species. The economic and ecological significance of sagebrush makes it very important to develop successful strategies for re-establishing it on abandoned mine sites and degraded rangelands. The transition of intact sagebrush ecosystems to ecologically damaged rangelands is especially problematic because it degrades wildlife habitat, reduced biodiversity and potentially alters ecosystem function (Davies and Svejcar 2008).

Here I assess the relationship between sagebrush recruitment and climatic events. Stem sections were collected from the following species: Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis* Beetle & Young), black sagebrush (*Artemisia nova* A. Nelson), low sagebrush (*Artemisia arbuscula* Nutt. ssp. *arbuscula*), and Lahontan sagebrush (*Artemisia arbuscula* ssp. *longicaulis* Winward & McArthur).

Stem sections were collected to provide information on the age of the stand, and I directly dated the years of successful recruitment through annual growth-ring analysis. Linking annual growth-rings of sagebrush to climate identifies climatic patterns responsible for recruiting new sagebrush cohorts. In Nevada, primary applications of this research include rehabilitation of mined lands, wildfire areas and habitat monitoring of sagebrush obligate wildlife species.
Recruitment of sagebrush cohorts was significantly correlated with climate variables, although the relationship varied by species or sub-specific identity. Recruitment in sagebrush populations occurred in pulses throughout Nevada and stand ages were significantly different (P<.001) among species and subspecies. Total precipitation the year prior to recruitment and the year following recruitment were reasonably good predictors of seedling establishment. Patterns in seedling establishment showed strong patterns in timing of recruitment pulses for individual species or subspecies, even though study sites were not located geographically close to one another.

The most interesting finding of this research was the significance of global climatic patterns. Monthly Pacific Decadal Oscillation (PDO) index variables were correlated with seedling recruitment in all species studied. This relationship was significant (α=.05) for low sagebrush at and Wyoming big sagebrush at each study site. July PDO was the most significant variable for low sagebrush at the Willow Creek Ridge site ($R^2=0.1058$, $P<0.0026$) and the Montana Mountain Site ($R^2=0.2188$, $P<0.0023$). April PDO was the most significant variable for Wyoming big sagebrush at the Antelope Valley site ($R^2=0.1459$, $P<0.0071$) and the Santa Rosa site ($R^2=0.1435$, $P<0.0248$). In general the shift from cool to warm phase of the PDO corresponded with increased sagebrush cohort recruitment (Figure 13, 14, 15 & 16). These results suggest that timing restoration efforts with the larger climatic environment may result in increased success.
Acknowledgements

First, I would like to thank my advisor Barry Perryman for having a great project ready to go when I inquired about graduate school. Barry has always been patient and provided me with great learning opportunities. I also want to thank my committee members Beth Ledge and Ben Bruce who provided editorial comments on my thesis. Beth was especially helpful, inviting me to participate in her lab meetings and providing advice when I needed it the most. Thanks also to my lab mates for the years of good times, listing to my problems and not minding the overwhelming smell of sagebrush in the lab. I also want offer a huge thank-you the field technicians Britney Askew, Erin Smith and Amanda Johnson for the hours spent cutting, sanding and counting. Finally, thank you to my friends and family for offering their assistance when needed.
# Table of Contents

Abstract..................................................................................................................................................i

Acknowledgements.............................................................................................................................iii

Table of Contents................................................................................................................................iv

List of Tables...........................................................................................................................................v

List of Figures........................................................................................................................................vi

Background...........................................................................................................................................1

Chapter 1.............................................................................................................................................7

Discussion...........................................................................................................................................27

Conclusions..........................................................................................................................................35
Chapter 1

List of Tables

Table 1: The ecological site, soil series and soil classification of each collection site.

Table 2: Topographic and climatic characteristics of each study site.

Table 3: A) Summary data of counts and ages for each species and site and B) ANOVA testing for differences between species and sites

Table 4. Species, subspecies, regional and stand R2 values from stepwise regression analysis. Significant individual R2 values denoted with an asterisk.
Chapter 1
List of Figures

Figure 1: Nevada map with study site locations.

Figure 2: Map of total annual precipitation in Nevada with MLRA boundaries.

Figure 3: Maximum, mean and minimum stand age for each species and site. Species and site code found in Table 1 and Table 2.

Figure 4: Negative distribution recruitment frequency plots with standard error bars and quantile box plots for each species and site. Quantile box plot shows smallest observation, lower quantile (25%), median (50%), upper quantile (75%), largest observation and the mean confidence diamond. The mean confidence diamond indicated the sample mean and 95% confidence interval.

Figure 5: Mean age by species. **A, B & C indicate statistically significant differences in species mean age.

Figure 6: Mean age by species and site.

Figure 7: A. arbuscula spp. longicaulis regional stand age frequency distribution.

Figure 8: A. nova regional stand age frequency distribution.

Figure 9: A. tridentata spp. wyomingensis regional stand age frequency distribution.

Figure 10: A. arbuscula spp. arbuscula regional stand age frequency distribution.

Figure 11: Example STM with restoration recommendations.

Figure 12: Sliding 5 years average of January, April, July, September, and November PDO index values.

Figure 13: A. arbuscula spp. longicaulis regional stand age frequency distribution with yearly PDO index.

Figure 14: A. tridentata spp. wyomingensis regional stand age frequency distribution with yearly PDO index.
Figure 15: A. nova regional stand age frequency distribution with yearly PDO index.

Figure 16: *A. arbuscula* spp. *arbuscula* regional stand age frequency distribution with yearly PDO index.
Background

The use of annual growth-rings to determine age structure in big sagebrush has been well established (Ferguson 1964, Roughton 1972 and Maier et al. 2001). Ferguson (1964) used dendrochronological methods to investigate multiple big sagebrush stands throughout the southwestern United States. Ferguson maintained that dendrochronological studies are useful in determining growth conditions affected by precipitation. Dendrochronology can be used to precisely date events. This dating is possible because ring widths are a record of variations in the local climate, favorable or unfavorable, dry or wet. Patterns of wide and narrow rings are visible on all woody plants growing in the area and can be used for cross dating (Fritts 1976). This process is called “dendroclimatogy”, or the science of reconstructing past climate with growth rings.

Sagebrush plants are generally long lived, therefore, it is not necessary for new individuals to recruit every year for perpetuation of the stand. Infrequent large recruitment events and simultaneous low, continuous recruitment is the foundation of population maintenance (Noy-Meir 1973). Although there is extensive knowledge of the importance of sagebrush ecosystems and on the deterioration of these systems, the processes and temporal patterns of recruitment in these systems are relatively unknown and may occur once a century (Ziegenhagen and Miller 2009). Research has previously investigated factors affecting the germination rate of sagebrush including temperature, seed moisture, seed size, and hours of day light (Busso et al. 2005, Booth...
2002, & Young and Evans 1989). However, there has been little research linking climate to successful recruitment of sagebrush seedlings. It is well known that sagebrush species are evolutionarily adapted to living in xeric environments. The influence of environmental variables on seedling establishment of sagebrush species in the field are largely unexplored (Davies et al. 2007).

Sagebrush species are characterized by a “pronounced delay in establishment” (Humphrey 1984). Patterns of plant succession following fire vary greatly by structural and functional group. Sagebrush is readily killed by wildfire and most species do not re-sprout. However, sagebrush systems of all types are able to easily perpetuate their stands where the natural fire return intervals have not been altered by invasive species (USDI-BLM 2002). The low mortality of bunchgrasses during fires indicates they do not need to be seeded, if they are present at the time of the fire. However, seeding native shrub species is ecologically important (James and Svejcar 2010) when remnant populations are not available to re-colonize following wildfire. Plants that rely on dispersal mechanisms or are not capable of vegetative reproduction, like sagebrush are the last major group to recover after fire (Humphrey 1984).

The historical disturbance regime of big sagebrush communities of the Great Basin included light grazing by large herbivores and an estimated fire return interval of 50 to >100 years (Davies et al. 2009). However, the historical disturbance regimes of the sagebrush steppe have not been maintained under European-style management.
Periodic low-to moderate-severity disturbances such as grazing and wildfire are needed to maintain ecological resilience and a balance between structural and functional groups (USDI-BLM 2002). Non-native annual grasses readily establish in this ecosystem today, promoting a fire return interval that is too narrow for native woody perennials to establish or reestablish in some cases. As a consequence of European settlements in the western U.S., much of the Great Basin has been heavily grazed for >100 years (USDI-BLM 2002). The modern invasion of non-native annual grasses in combination with decades of inappropriate management has resulted in degraded sagebrush ecosystems.

The management perspective of sagebrush has evolved over several decades of rangeland management (Lommasson 1948). Sagebrush was initially considered undesirable by the ranching industry, due to its propensity to increase under grazing management techniques of the time. Since settlement began in the West, sagebrush ecosystems have been degraded or eliminated due to agriculture conversion, poorly-managed livestock grazing, introduction of non-natives, oil and gas development, mining, fire management activities, urban sprawl, water diversion, pinyon-juniper encroachment, off road vehicles, linear corridors and wildfire cycle behavior (USDI-BLM 2002). Today, changes in fire-return intervals, combined with knowledge of the central role sagebrush plays for wildlife habitat, have helped renew interest in seed propagation for this genus.
Nevada receives very little growing season precipitation. For the majority of the year temperature and precipitation are negatively correlated and most precipitation arrives when it is too cold for plants to utilize it. This can be detrimental for sagebrush seedlings because when temperature is at its highest, precipitation and soil moisture are much lower. The need for spring and early summer rains may not be independent of the effect of spring time temperature regimes and seedling growth rates (Cawker 1980). Adequate soil moisture and correct timing of germination minimizes exposure to prolonged high temperatures and increases recruitment (Beetle 1960). If climatic fluctuations affect recruitment success in stands of sagebrush, these fluctuations will be recorded in the population age structure and the growth-rings. The probability of recruitment for an individual is subject to the climate conditions the year the seed germinated, as well as at least one year following (Cawker 1980). This means that sagebrush seedlings are vulnerable to suboptimal weather conditions, as well as other environmental variables until they are well established.

Maier et al. (2001) concluded that sagebrush establishment is highly dependent on the timing and amount of precipitation, although they found some variability among subspecies. This study further investigates the relationship between successful sagebrush cohort establishment and timing and amount of precipitation, as well as other precipitation-related variables across Nevada. Conventional approaches assume ecosystem processes are continuous and regulated by smooth inflow/outflow relationships (Schwinning and Sala 2004), but semi-arid ecosystems do not fit well into
this model. They are characterized by discontinuous and highly variable rainfall events that control ecosystem processes (Schwinning and Sala 2004). The time between events allow soil nutrients to build up, increasing the biological response to longer more sustained events. This relationship maintains that only certain weather events are responsible for species recruitments, establishment and survival.

Depth of soil moisture also varies by pulse durations: the deeper the pulse, the lower the amount of evaporation. Deeper pulses also contribute to increased plant water uptake. Pulse depth is strongly correlated with changes in soil texture and precipitation amount (Schwinning and Sala 2004). Greater soil moisture availability leads to increased annual growth. In adult sagebrush plants, increased annual growth is represented in the size of annual growth-rings. Large rainfall events are quite variable from year to year and are likely a major source of among-year variability in the ecosystem. It is reasonable to assume large recruitment events are correlated with large increases in available soil moisture, since they are also characterized by high variability among years.

**Thesis summary:**

This thesis addresses three objectives related to the survival of *Artemisia* species on arid rangelands, specifically, I:

1) Investigated the demographic characteristics of four *Artemisia* species and subspecies.
2) Examined how particular climatic variables or trends in precipitations affected the establishment and success of new *Artemisia* cohorts.

3) Developed guidelines for land managers relating to methods and timing of sagebrush seeding.
Chapter 1

Keywords: Artemisia, sagebrush, seedling recruitment, pulse recruitment, climate, precipitation, arid rangelands

INTRODUCTION

Sagebrush Distribution and Importance:

Sagebrush (Artemisia spp.) species are likely the most common shrub in North America (Meyer 2008). This widespread genus is well adapted to life in arid environments, especially in the Great Basin, and has been described as the most important shrub in North America (Beetle and Johnson 1982). Sagebrush is found on an estimated 153 million acres (~61,916,900 ha) of the western U.S. and 17.3 million acres (7,000,000 ha) of the Great Basin (Loik and Redar 2003). Big sagebrush (A. tridentata Nutt.) alone occupies an estimated 60,000,000 ha (148,263,230 acres) as a landscape dominant or co-dominant (Meyer 2008). This circumboreal genus is commonly found on well drained soils, generally aridisols, in areas with cold winters, and low precipitation (typically 200-700 mm) that predominantly comes during the winter months. It is the dominant vegetation on much of the Columbia River Plateau, the Great Basin, the Colorado Plateau and western Wyoming. The fossil record and records from early pioneers indicates that sagebrush has existed in its approximate present day distribution for 1.2 million years (Tidewell et al. 1972 and Barnosky et al. 1987).

The Artemisia genus is divided into species and subspecies by differences in growth form and morphology. Differences in grazing value and habitat characteristics are important when determining how species and subspecies will respond to
management (Beetle and Johnson 1982). Different species of sagebrush have different palatability and structural characteristics that influence their use preference by different wildlife species and domestic livestock.

Black sagebrush (A. nova A. Nelson) in Nevada is commonly found on sites with shallow calcareous soils and an impervious caliche layer (Table 1). Black sagebrush sites are dryer and more saline relative to those of other Artemisia species and can be closely associated with the salt desert shrub community. It is especially important on low elevation winter ranges where extended snow free periods allow wildlife to utilize the plant through most of the winter (McMurry 1986). Wyoming big sagebrush (A, tridentata ssp. wyomingensis Beetle & Young) is the most drought tolerant of the big sagebrush subspecies and will grow on a variety of soils (Howard 1999) (Table 1). Commonly associated species throughout Nevada include fourwing saltbush (Atriplex canescens), rubber rabbitbrush (Chrysothamnus nauseosus) or blackbrush (Coleogyne ramosissima). It also occurs as dominant understory shrub associated with pinyon-juniper woodlands. Low sagebrush (A. arbuscula Nutt. ssp. arbuscula) is a highly preferred forage plant by large wildlife, as well as an extremely important food item for sage grouse. Distribution of Lahontan sagebrush (A. arbuscula ssp. longicaulis Winward & McArthur) is mostly limited to Nevada, California, and Oregon. Areas where it occurs only receive 6.8-13.7 inches (175-350 mm) of precipitation annually, mostly as snow in the winter months. Lahontan sagebrush occurs on similar soil types as low sagebrush;
generally these soils have low water holding capacity with an argillic horizon at a relatively shallow depth (Winward and McArthur 1995) (Table 1).

Sagebrush is very important for soil stabilization and wildlife habitat. It provides forage for domestic sheep, mule deer and pronghorn antelope (Tirmentstein 1999). Almost 100 bird species depend on the sagebrush ecosystems for their habitat needs. An additional suite of species are considered sagebrush obligates, these include sage grouse, sharp tailed grouse, sage thrashers, sage sparrow, Brewers’ sparrow, horned larks and pygmy rabbits. The evergreen leaves of sagebrush provide important winter forage for black tailed deer, white tailed deer, elk, bighorn sheep, and jackrabbits (USDA-NRCS 2011). Domestic livestock, such as cattle, will also forage on sagebrush when more desirable forages are unavailable.

Sagebrush species have been seeded to improve big-game winter range and to rehabilitate mined lands for more than 30 years (Meyer 2008). When reintroducing native vegetation to a site it is important to choose the species or sub-species that are best suited to those site characteristics. The USDA-Natural Resources Conservation Service (NRCS) provides specifications and standards for rangeland seedings. These guidelines include a soil suitability rating, guidance for selection of plant materials, seed bed preparation, seeding rates and planting methods. Species chosen for rangeland seedings are based on the specific objectives of the project. In sagebrush systems, the objective is often to provide wildlife habitat and soil stability. Therefore, it is strongly
recommended that seed mixes are designed for the reference plant community of that ecological site as defined by the site description (USDA-NRCS 2010).

**Sagebrush Ecology:**

Most sagebrush species depend on seed for regeneration, as few species have the ability to sprout from the root crown following wildfire or other disturbance (Meyer 2008). Typically, sagebrush species flower in late summer or autumn and ripen from September through December. The tiny yellow-brownish flowers are wind pollinated (Meyer 2008). Fruits are shaken from the plant by wind within a few weeks of maturation. Seeds are very small (.15 to .25 mg) (Busso et al. 2005) and can be distributed by the wind, but commonly fall close to the parent plant. A single adult sagebrush plant is capable of producing hundreds of thousands of seeds in a single year (Meyer 2008).

Information on germination requirements of sagebrush is limited to a few species, but evidence suggests that sagebrush species require cold stratification in order to germinate. Timing mechanisms are keyed to a pattern of winter or early spring germination and early spring emergence for all species examined so far (Meyer 2008). Timing of germination response is tied to climatic variables at the collection site. For example, seeds from populations from high montane environments with long, cold, snowy winters tend to be slower to germinate. Such traits protect seeds from germinating too early before conditions are ready (Meyer 2008). Maier et al. (2001) hypothesized that in northeast Wyoming, persistent winter snow cover may serve to
protect young plants from winter desiccation. The snow also provides additional soil moisture during snowmelt, contributing to the overall size of the resource pulse when snow melts in the spring time.

Young and Evans (1989) found the highest number of germinable seeds in the soil was found one month after initial seed dispersal, in December. This study was geographically located in the northwestern Great Basin, on disturbed sites dominated by cheatgrass (*Bromus tectorum*). An unusual rainstorm occurred in 1986, year four of the study. After this rainstorm, a substantial amount of sagebrush seedling emergence was recorded, in some places as much as 100 fold increases from the previous year. They found that sagebrush seedlings emerged every year, but would die before or by June. This indicates that sagebrush seedling emergence is correlated with precipitation and that further summer precipitation maybe required for seedling survival.

Most big sagebrush seeds germinate during the winter or spring following their production. Seeds are not especially long lived in the soil; reports from the field vary from one to four years (Ziegenhagen and Miller 2009, Booth 2002, Young and Evans 1989). Seeds stored in a warehouse only retain full viability for two to three years (Meyer 2008). Successful recruitment depends on a good seed production year, followed by the right conditions for recruitment and survival. The goal of this research is to identify the relationship between climate variables and cohort recruitment in
sagebrush stands in Nevada, and to determine if these relationships varied among species

The most critical time for precipitation are the months immediately following initial seedling emergence. More than half of all germination in a given year occurs in less than a week, indicating that seedling viability is greatly dependant on soil moisture in the time immediately following initial germination (Busso et al. 2005). Booth et al. (1990) discovered Wyoming big sagebrush achieved its highest growth rate soon after germination, suggesting that this species is adapted to use water when it is most available. High spring growth rates in seedlings are likely an attempt to develop a root system that will be able to survive a prolonged summer drought (Booth et al. 1990).

It is well known that species and subspecies of sagebrush commonly hybridize. Hybrids typically arise from the proximity of populations of different taxa. This area of proximity is called an ecotone. Ecotones serve as a bridge of gene flow between species populations and add to the plasticity that allows sagebrush species to occupy a wide ecological niche (McArthur and Sanderson 1999). Hybrids can be particularly well suited to inhabiting an ecotone considered undesirable to the parent species, this helps to develop pure stands. Pure stands of stable hybrids provide a reservoir of fit individuals, increasing established species of *Artemisia* fitness as a landscape dominant (McArthur and Sanderson 1999). It is suggested that Lahontan sagebrush is the offspring of low sagebrush and Wyoming big sagebrush (Winward and McArthur 1995). Morphologically
it differs from low sagebrush with its long floral stalks and larger leaves. Hybridization is also believed to have resulted in other widespread species of sagebrush such as Wyoming big sagebrush (Winward and McArthur 1995).

**Factors affecting rehabilitation:** Many strategies have been tested for improving the establishment rates of *Artemisia* seedings. These include sowing sagebrush with other shrubs, with facilitating grasses, various surface seeding techniques, topsoil management, and sowing in combination with snow catchments and mulching (Booth 2002). Sagebrush has been also grown as bare-root and container stock. However, transplanting can be precarious, as moisture conditions must be ideal and plants require careful hardening (Meyer 2008). Sagebrush is one of the few native shrubs that can be reliably direct seeded, either by broad-cast or drill seeding. However, research has shown that only four percent of seed applied in a seeding germinates and emerges (James and Svejcar 2010). Restoration practices could benefit greatly from added knowledge about the episodic nature of sagebrush recruitment identified by Maier et al. (2001) and Perryman et al. (2000). Previous research has concluded that seeding efforts are sensitive to timing and techniques, but included no specific information about practices that result in successful rehabilitation efforts. The research conducted by this study is needed to ensure ecologically significant species such as sagebrush are not lost.

Multiple factors affect seedling survival (Gillespie & Loik 2004). In arid and semi-arid ecosystems water is the most limiting resource, but all biological resources go
through periods of high and low abundance. In desert ecosystems pulses of high resource availability are usually triggered by rainfall events (Schwinning & Sala 2004). Several theories have emerged over time to understand how precipitations events affect water limited environments. Water, unlike most nutrients, flows through the system. Very little water is recycled by plants or animals, or returned to the system in the form of dew (Noy-Meir 1973). Arid systems are therefore unable to carry out biological functions requiring water, without new inputs. Precipitation or rainfall events become the driving variable because they are not controlled by factors within the local systems (Noy-Meir 1973). Since the driving variable occurs in pulses the response of the biological system also occurs in pulses. Timing of rainfall events is central to successful native plant recruitment and survival.

Due to the wide ecological amplitude of sagebrush it is a common choice for restoration in Nevada and across the arid west. In the center of the species geographical niche, sagebrush is found of the widest variety of sites (Fritts 1976). Species used for restoration should be chosen with respect to their natural moisture and elevational gradients (Mahalovich and McArthur 2004). Wyoming big sagebrush typically receives less than 305mm (12 inches) of precipitation annually (Table 2), is tolerant of droughty and saline conditions and is valuable for stabilizing slopes and gullies and (Howard 1999). It is likely the most damaged sagebrush habitat type in the West. Black sagebrush is adapted to drier sites and is recommended for restoration in sites that receive less than 175.26 mm (6.9 inches) of rainfall annually (McMurray 1986). Establishing
seedlings within zones of limited precipitation is extremely difficult. Matching species or subspecies to its native elevation and precipitation range (Table 2) increase the survival and reproductive success of reclamation attempts (Mahalovich and McArthur 2004).

I tested the following hypotheses: 1) Climatic variables such as quarterly precipitation, total annual precipitation in the year of recruitment, total precipitation in the year prior to recruitment, total precipitation in the year following recruitment, average annual dewpoint and PDO index (Pacific Decadal Oscillation) affect the establishment of sagebrush seedlings in native rangelands in Nevada; 2) important climatic variables are not be the same for all species or subspecies studied. Climatic variables are not expected to have same influence on all species and subspecies of Artemisia. We predicted precipitation would be most significantly correlated with sagebrush recruitment, though which precipitation variable is most important may vary by species. We hope to more fully explain the influence of precipitation on the establishment of Wyoming big sagebrush, black sagebrush, low sagebrush and Lahontan sagebrush, as research thus far has had little success in clarifying these complex relationships.

RESEARCH METHODS

The research methods consisted of four components: 1) Collection shrub stem sections of four species and subspecies of sagebrush (A. nova, A. arbuscula ssp. arbuscula, A. arbuscula ssp. longicaulis and A. tridentata ssp. wyomingensis); 2)
Preparation and counting of the stem sections; 3) Collection climatic data from weather stations near study sites; 4) Use of linear regression and multiple stepwise regression to determine the most significant precipitation variable or variables.

Site selection:

Study sites were chosen to represent different locations where the species or subspecies of interest naturally occurs (Figure 1). Stands were chosen if they appeared to have multiple cohorts, were similar in topography, soil and landscape position, relatively free from disturbance (such as recent wildfire or excessive grazing), and not in close proximity to other species of sagebrush to avoid cross breeding. Areas large enough to sample three 100x100m plots were selected for this project. In some locations, individual 100x100m plots making up the regional stand were located within a five mile radius. Species and subspecies were identified using keys, technical notes and special publications, including Common Sagebrush in Nevada (Schultz and McAdoo 2002), Lahontan Sagebrush: A New Taxon (Winward and McArthur 1995), Key to Species of Sagebrush (Shultz 2007), Sagebrush Identification, Ecology, and Palatability Relative to Sage-Grouse (Rosentreter 2005) and Key to some Taxa of Artemisia in Nevada (Plummer 1986).

A search of the homestead records was conducted for all collection sites after sampling by searching the BLM database of land patents (http://www.glorecords.blm.gov/). The database was searched by location using the
township, range and section (T R S) (Morris 2011). A record of farming was discovered and the corresponding homestead record was ordered from the National Archives and Records Administration (NARA) (www.archives.gov). Homestead records provide information from the United States Land Office including the first individual to file a homestead record, what year they began farming the land and what type of crops they planted.

**Sampling:**

For each species, 80 stem sections were collected per stand, with three stands sampled per site. Data was collected from two sites for each species or subspecies. The project includes 36 stands total (6 stands per species or subspecies) for approximately 1920 total stem-sections collected.

A stratified, random sampling method was used to collect stem cross-sections from each sagebrush stand. A 100 meter long baseline transect was located within each stand and ten 100m long perpendicular transects were established at randomly selected points along the baseline transect. Along each perpendicular transect, eight random points were selected and the closest individual sagebrush plant that met the sampling criteria was collected (n=80). This method follows the sampling criteria laid out by Roughton (1972). Individuals sampled were limited to those with intact stems. When an appropriate plant was found the stem section was obtained by sawing the plant off below the root crown, to ensure that the pith and the first annual growth-ring were
included. Many older plants lacked radial symmetry. The oldest individuals in a stand often lay on the ground, which leads to exposure of the pith and deterioration of the stem. It was not possible to determine the true age of such plants, so our sampling method was biased to single stem plants with intact piths (Perryman et al. 2001). This design element leads to the exclusion of the oldest individuals within a stand. Samples, including the root crown and a portion of the above ground stem, were then taken to the laboratory. In the lab, a table-top vice was used to secure each stem section while a hacksaw was used to cut at the root crown. Cut stem sections were sanded with progressively finer grit sand paper (120-220-320 grit) on an electric belt sander. Annual growth-rings were examined using a 10-power stereomicroscope and counted by two individuals. Artemisia species can be difficult to count because growth form is highly irregular. Stem-sections easily rot in the center, split along the side, and can have lobes of growth on one side only. The first annual growth ring is visible due to their light color and small size. When the two initial observations disagreed the stem-section was sanded again with progressively finer sandpaper and counted a third and final time. True ages were counted from the pith to the live cambium at the edge of the stem cross-section.

**Climate:**

Many of the weather stations located in desirable proximity to the study sites did not have a continuous record. In some cases, days or weeks were missing, others were missing entire decades. Due to being unable to locate study areas near weather
stations with a long-term reliable record, Parameter-elevation Regressions on Independent Slopes Model (PRISM) climate group data was utilized (Daly et al. 1994). PRISM climate information is based on point precipitation and temperature measurements, as well as, knowledge of rain shadows, temperature inversions, orographic and coastal effects. PRISM is particularly well suited for this study because it includes a conceptual framework that addresses orographic precipitation patterns in mountainous regions (Daly et al. 1994). Collective climatic information expressed in terms of means, variance and extremes for a particular region for a period of many years is considered to be the macroclimate (Fritts 1976). Data used to develop a confident estimate of the macroclimate of a region is often based on 30 or more years of actual records (Fritts 1976). A map of the annual precipitation ranges across Nevada is available in Figure 2.

Monthly averages of precipitation were generated for each site and monthly averages were grouped into quarterly totals to represent growing seasons. Generally, there are consistencies in monthly precipitation variables especially in regions where winter precipitation is greater than summer precipitation (Noy-Meir 1973). Quarters were chosen based on moisture availability to plants and phenological stage of plant: March-April-May, June-July-August, September-October-November, and December-January-February. Totally annual precipitation variables were also generated for the year prior to recruitment, the year of recruitment, and the year following recruitment. Additional variables included in the analysis include average annual dewpoint and PDO
Dewpoint is the temperature to which a parcel of humid air must be cooled for water vapor to condense into water. It is important because evaporative demand is much lower under cooler and more humid conditions. The PDO index is a measurement of sea surface temperatures, sea level pressure and surface windstress. Monthly temperature variables (maximum, minimum and average) were initially included in regression analysis, but removed when determined they did not change the statistical significant relationships.

PDO is described as a long-lived El-Nino-like pattern of Pacific climate variability (Mantua 1999). Like El-Nino, PDO influences variability in large-scale climate patterns over North America. However, PDO events persist for 20 to 30 years, while El-Nino events typically last for only 6 to 18 months and the climatic signature of PDO is most visible in the North Pacific/North American sector while secondary signatures exist in the tropics, the opposite is true for El-Nino (Mantua 1999). PDO index is useful in predicting extreme variations in the weather patterns of a particular region, such as droughts or floods (Zhang et al. 2010 and Benson et al. 2003). Monthly PDO index values used in the regression analysis include January, April, July, September, and November.

**Statistical analysis:**

Stem section counts (3 stands/site, 2 sites/species, and 4 species) were compiled by site and species. Differences between mean species ages at each site were compared
using a one way analysis of variance (ANOVA) with species and site (nested within species) as model factors.

Frequency distributions were used to determine the percent of stand recruitment within the period examined by the stem sections collected. Percent of total recruitment per year was calculated by dividing the total number of stem sections collected at a site by the frequency of individuals at a specific age.

Multiple linear regression analysis was used to study the relationship between percent of cohort recruitment in a given year and precipitation variables. All relationships were tested for significance at $\alpha=0.05$. The independent variables or precipitation variables included quarterly precipitation totals (March-May, June-Aug, Sept-Nov, and Dec-Feb), total precipitation during the year of recruitment, total precipitation year prior to recruitment, total precipitation year following recruitment, average annual dewpoint and January PDO, April PDO, July PDO, September PDO and November PDO. Many PDO index variables were highly correlated. To correct the issue of multicollinearity variables with multivariate correlations greater than .75 were removed from the analysis. February PDO, March PDO, May PDO, June PDO, August PDO, October PDO, and December PDO exhibited high multicollinearity and were not used in the regression analysis. Correlation between remaining variables was determined to be minimal. Independent variables were used to predict the dependant
variable, percent of total recruitment in a given year, through multiple linear regression analysis.

Multiple stepwise regression was used to investigate the relationship between percent of recruitment per year and climatic variables. Stepwise regression is a technique known as a variable screening procedure (pg 322 Mendenhall and Sincich 2003). It is used to objectively determine which independent variables (X- weather variables) are the most important predictors of the dependent variable (Y - percent of recruitment per year) and which are the least important predictors. The independent variable that produces the largest absolute ‘t’ value is declared the best one variable predictor of Y. Additional independent variables are added and it is determined if they add to the significance value of ‘t’. If not the variable is removed.

RESULTS

Demographic Analysis of Stands:

Demographic analysis of the species or subspecies of sagebrush examined by this study indicate episodic recruitment. Stand ages were significantly different (α= 0.05) at the species level and at the site level (p<0.001) (Table 3). Mean stand ages varied by species (Figure 5) and sites differed for Wyoming big sagebrush and black sagebrush (Figure 6).

Black sagebrush stands had the oldest average age of all individuals sampled. The oldest individual at the Red Peak site was 77 years, the youngest 3, and the mean
27. Black sagebrush at the Spring Valley site had a similar cohort structure the oldest individual was 73 years, the youngest 4, and the mean 25 (Figure 3).

Wyoming big sagebrush had the oldest individual plant sampled. At the Antelope Valley site the oldest individual was 79 years old, the youngest 2 and the mean 27. The maximum age at the Santa Rosa study site was much younger. The oldest individual was 40 years. However, the youngest was 6 and the mean was 21, similar to the Antelope Valley study site (Figure 3).

Lahontan and low sagebrush had similar maximum, mean, and minimum ages. The oldest individual Lahontan sagebrush plant was at the Oat Mountain study site at 57 years, the youngest 11, and the mean 20. The oldest plant at the Antelope Flat study site was 40 years, the youngest 6, and the mean 20. Low sagebrush had the youngest average age of all species and subspecies sampled. The oldest plant at the Willow Creek Ridge study site was 49 years, the youngest 8, and the mean 19. The oldest plant sampled at the Montana Mountain study site was 40 years, the youngest 5 and the mean 18 (Figure 3). Different aged cohorts found in particular stands were not spaced on regular yearly intervals and these intervals are not repeated across the landscape (Figure 7, 8, 9 & 10).

**Percent of years with recruitment:**

Pulse recruitment of sagebrush stands is characterized by a negative binomial distribution. The period of time examined by the stem-sections collected in this study is
characterized by a large percentage of years with little to no seedling recruitment in all species and subspecies of sagebrush studied. There are many years with little to no recruitment, a several years with a moderate amount of recruitment, and few years with a large pulse of recruitment (Figure 4).

**Regional stand age frequency distributions:**

Individual stem sections were examined to determine the frequency of individuals at a specific age on a regional level. Histograms of regional stand age frequency distribution compare patterns of species and subspecies recruitment. These histograms show the patterns of pulse recruitment are similar for specific species or subspecies regardless of the study site (Figure 7, 8, 9 and 10). I found large pulses of recruitment occurred around the same time for both study locations for each species or subspecies studied.

**Multiple Stepwise Regressions:**

Cohort recruitment appears to be correlated with weather variables, although specific relationships varied by species and location (Table 4). Important weather variables included summer precipitation, total precipitation year of, the year following and the year prior to recruitment, average annual dew point and the PDO index.

**A. nova:**

Recruitment of black sagebrush at the Spring Valley study site was most correlated with April PDO, followed by average annual dewpoint, September PDO, total
annual precipitation and July PDO ($R^2=0.2850$). None of the independent variables were significantly correlated with recruitment at the Spring Valley study site. Multiple stepwise regression showed black sagebrush at the Red Peak site was most significantly correlated with total precipitation the year following germination, followed by total precipitation the year prior germination, April PDO and June through August precipitation ($R^2=0.5176$). Linear regression indicated that the independent variables of total annual precipitation the year prior ($R^2=0.2558$), year of ($R^2=0.2627$) and year following ($R^2=0.2628$) recruitment were all significantly correlated with recruitment at the Red Peak study site (Table 4).

**A. tridentata ssp. wyomingensis:**

Wyoming big sagebrush at the Antelope Valley study site was most correlated with total precipitation the year of recruitment, followed by July PDO and precipitation from December through February ($R^2=0.2522$). Individual linear regression showed that June through August precipitation ($R^2=0.096$) and September through November precipitation ($R^2=0.1112$), total annual precipitation ($R^2=0.1684$) and all of the PDO index variables were significantly correlated with recruitment at the Antelope Valley study site. Wyoming big sagebrush at the Santa Rosa Mountains study site was correlated with total precipitation year prior to recruitment, followed by April PDO, precipitation from March through May, precipitation from June through July, July PDO and January PDO ($R^2=0.6051$). Individual linear regressions showed that total precipitation year prior to recruitment ($R^2=0.3655$) and April PDO ($R^2=0.143$) were
significantly correlated with recruitment at the Santa Rosa study site. July PDO was significantly correlated to recruitment at both Wyoming big sagebrush study sites (Table 4).

There was a record of historic dry-land farming at the Santa Rosa study site. Implications of this include modification of the soil profile. The property was homesteaded beginning in 1914. Although native species have had sufficient time to recover, plowing and other farming practices have long-term impacts on the site.

*A. arbuscula ssp. arbuscula*:

Low sagebrush recruitment at the Willow Creek Ridge study site was most correlated with July PDO \( (R^2=0.1058) \). Low sagebrush at the Montana Mountain study site was most correlated with July PDO, followed by November PDO, average annual dewpoint and precipitation from December through February \( (R^2=0.3669) \). Individual linear regressions showed that July PDO and April PDO were significantly correlated with recruitment at both low sagebrush study locations (Table 4). Recruitment at both study sites was most correlated to the positive phase of PDO.

*A. arbuscula ssp. longicaulis*:

Stepwise multiple regression showed that recruitment of Lahontan Sagebrush at the Antelope Flat site was most correlated with July PDO, followed by December through February precipitation, April PDO, January PDO and November PDO \( (R^2=0.3439) \). Stepwise multiple regression showed that recruitment of Lahontan sagebrush at the
Wild Oat Mountain showed July PDO was correlated with recruitment ($R^2=0.0656$).
Recruitment at both study sites was most correlated to the positive phase of PDO.

**DISCUSSION**

The primary goal of this research was to indentify the climatic patterns related to sagebrush seedling recruitment on native sites in Nevada. Comparing years of successful cohort establishment with historic weather data provided the basis for identifying the preferred climatic conditions for recruitment of sagebrush seedlings into native undisturbed sites. Previous research indicated large pulses of sagebrush germination in response to cool, wet conditions (Booth 2002, Young and Evans 1989). Successful recruitment in stands of big sagebrush has been positively correlated with variations in local precipitation in Wyoming. Positive indicators include above-average winter precipitation and growing season moisture (Maier et al. 2001). We expected available precipitation to be more important than temperature when predicting sagebrush recruitment in Nevada, our results did support this hypothesis. Additionally, the PDO index which affects larger global climate patterns, was often correlated with recruitment (Table 4). ANOVA results indicated species and stand mean ages were significantly different (Table 3). Therefore, we can conclude that landscape level factors, such as local and global weather patterns are driving recruitment.

Annual growth-ring analysis was used to determine age of individual stem-sections which were then analyzed against precipitation variables. Annual growth ring
analysis was ideal for this study because *Artemisia* is considered to have sensitive growth rings, meaning they show variation from ring to ring as a result of the climate (Fritts 1976) p 19. The climatic information used in this study includes the Parameter-elevation Regressions on Independent Slopes Model or PRISM data, developed by the Spatial Climate Analysis Service at Oregon State University. There are obvious limitations associated with using modeled climate data, instead of data from nearby weather statations. However, climate records can also be in error if there are relatively few observations for a particular weather station or if the station locations are not representative of the study site (Fritts 1976). Western Region Climate Center (WRCC) weather stations were not used because many of the stations of interest were not representative of the sample site or the period of record was too short or missing observations.

Overall, individual plant age and stand ages in this study were younger than those found in other sagebrush dendrochronology studies (Perryman et al. 2001, Ferguson 1964 and Cawker 1980). The oldest individual (79 years) was a Wyoming big sagebrush plant from the Antelope Valley study site. Mean stand ages ranged from 27 to 18 years (Figure 3). Perryman et al. (2001) examined big sagebrush stands in Wyoming and found slightly older individuals ages (81 years) and mean stand ages (32 to 17 years). Big sagebrush stem-sections collected by Ferguson (1964) across the southwestern United States were frequently greater than 100 years of age. This study was designed to collect the oldest individual sagebrush plants in a stand in order to
evaluate the rate of “annual lateral growth of the stems of big sagebrush” (Ferguson 1964 p.1). Dendrochronology experiments are purposely stratified to gather observations from the populations that contain the desired information (Fritts 1976). For the purposes of this study the first annual growth rings are a particular interest in order to determine the year of establishment. It is likely there were older individuals at the study sites I sampled, but the smaller sagebrush species examined here tend to have a lower growth form, which over time results in a larger proportion of the plants rotting and losing the first annual growth rings.

Nevada has great climatic diversity due to the highly variable topography, with valley bottoms as low as 1,500 ft and mountain ranges as high as 10,000 ft. Thus, we expect to see unique climatic relationships for each of the species studied. Precipitation averages 228 mm (9 inches) in the lowlands, mountains experience heavy snow fall and daily temperature can vary wildly. Majority of precipitation arrives during the winter in the form of snow (WRCC 2009). Cold season precipitation events accumulate to produce a single large pulse when snow melts in the spring and early summer. The success of primary producers in arid regions is the direct result of precipitation events at particular points in time and subsequent variation in rainfall over a region influences the local success for that particular region (Beatley 1974). Large disparities in the spatial distribution of rainfall across Nevada results from the mountainous terrain and this relationship was evident in my results. Species and subspecies collection from the higher elevation study sites had consistently higher R² values resulting from the multiple
stepwise regressions (Table 4). The higher elevation study sites receive more annual precipitation (Table 2), and thus may show a stronger relationship between recruitment and precipitation. It is logical to assume similar relationships are occurring at the lower elevation study sites, but the limited annual precipitation in combination with other local factors reduce the statistical significance of the relationship.

During extended dry periods the ecosystem achieves an inactive or steady-state (Noy-Meir 1973). During inactive periods little to no recruitment occurs and woody species develop negligible growth-rings widths. Soil moisture regimes associated with the sagebrush ecosystem are generally Aridic, which means soils are dry for more than 50 percent of the growing season and do not stay moist for as long as 90 consecutive days during the growing season. Sagebrush also occurs in soil with a Xeric moisture regime, these soils are characterized by large water deficits in the summer (USDI-BLM 2002). Soils with Xeric moisture regimes are dry in all horizons for 45 or more consecutive days in the four months following the summer solstice (Soil Survey Staff 2010). All study sites included in this project typify Aridic, Aridic bordering on Xeric, or Xeric soil moisture regimes (Table 2). The two lowest $R^2$ values ($R^2=0.1058$ at WCR, $R^2=0.285$ at SV) were characterized by Xeric moisture regime. Recruitment at two sites were not significantly correlated with any of the independent variables, Spring Valley and Antelope Flat, both were on Xeric soils. In these locations soil conditions may overwhelm global weather patterns and local conditions and therefore determine recruitment patterns. Results indicate recruitment is correlated with precipitation
variables. However, not all species exhibited the same relationship (Table 4) species differed in their sensitivity to each precipitation variable.

**A. nova:**

The precipitation the year prior to recruitment was important for survival in black sagebrush at the Spring Valley ($R^2=0.002$) and the Red Peak ($R^2=0.256$) study sites (Table 4). This relationship is expected because precipitation is directly related to seed production. The number of seeds and size of seed heads on a particular sagebrush plant is directly related to the quality of the site and the amount of precipitation that year (Beetle 1960). Precipitation the year following recruitment was significant at the Red Peak study location ($R^2=0.263$) (Table 4). I expected to see this relationship carry across most species since seedlings easily succumb to droughty conditions during the first year, however my results did not support this. December through February precipitation was important for black sagebrush at the Spring Valley study site ($R^2=0.050$) (Table 4). At the Spring Valley site December through February precipitation comes as snow and I hypothesize it could protect the seedling from extremely low winter temperatures. The percent of recruitment increased with increasing precipitation for all relationships. The importance of April PDO and total annual precipitation the year of germination at both study sites is a significant commonality. The overall greater significant relationships at the Red Peak study site are likely a consequence of the more favorable local conditions, including the soil moisture regime.

**A. tridentata spp. wyomingensis:**
Total annual precipitation the year of recruitment was significantly correlated (α=.05) with percent of recruitment within stands of Wyoming big sagebrush at the Antelope Valley study site ($R^2=0.1684$) (Table 4). Individual linear regressions also showed that June through August precipitation ($R^2=0.096$), September through November precipitation ($R^2=0.1112$), and all the PDO variables were significantly correlated with recruitment at Antelope Valley (Table 4). I hypothesize that summer and fall precipitation were significantly correlated with recruitment at the Antelope Valley location because precipitation patterns in eastern Nevada are strongly influenced by the summer monsoonal pattern of the Mojave and Sonoran Desert. Precipitation the year prior to recruitment was significantly correlated with recruitment of Wyoming big sagebrush at the Santa Rosa Mountain study location ($R^2=0.3655$) (Table 4). As with the other species, I hypothesize precipitation the year prior to recruitment is important for seed production. Percent of recruitment increased with increasing precipitation for all relationships.

April PDO was significant at both of the Wyoming big sagebrush study sites (Antelope Valley; $R^2=0.129$) (Santa Rosa; $R^2=0.143$) (Table 4), indicating that large climate patterns affect recruitment of this species. Recruitment at both study locations was most correlated with the positive phase of PDO.

The homestead record for the Santa Rosa study site states that the land was seeded with brome grass, irrigated and used for pasture. Associated grass species
recorded during the sampling of this site include squirreltail, bluebunch wheatgrass, Thurber’s needlegrass and Great Basin wildrye. The presence of these native grass species and the mature stand of sagebrush indicate the site has had adequate time to recover from the farming disturbance. However, the natural pattern of recruitment may be affected by the extensive soil disturbance. The effect may have been positive, i.e. native species readily established here after it was no longer farmed because the seedbed had been prepared.

The oldest individual at the Santa Rosa study site was much younger than the other Wyoming big sagebrush study site, Antelope Valley, with the maximum age at Antelope Valley 79 years, compared to only 40 years at the Santa Rosa study site (Figure 2). However, the plants were not visibly smaller in diameter or height. The cohort recruitment pattern for Wyoming big sagebrush was similar regardless of site location or historic disturbance (Figure 9).

*A. arbuscula* spp. *arbuscula*:

July and April PDO were significantly correlated with recruitment of low sagebrush at the Montana Mountain study site ($R^2=0.3669$) (Table 4). July PDO was also significantly correlated with recruitment at the Willow Creek Ridge Study Site. Specifically, percent of recruitment increased with the positive phase of PDO. I hypothesize that soils with an argillic horizon which low sagebrush prefers play a role in available soil moisture during the spring and summer. The strong argillic or clay layer
can cause water to be held above the texture change until that horizon becomes saturated (Davies et al. 2007), resulting in a perched water table during heavy precipitation events. Species with shallow roots may be more likely to utilize precipitation from spring events before it evaporates (Fetcher and Trlica 1980). A perched water table will strengthen this relationship creating an advantage for shallow rooted species or shrub seedlings when water is held in the upper profile.

**A. arbuscula spp. longicaulis:**

Seasonality of precipitation was important for these study sites, but there is not an easily identifiable pattern to the relationship. None of the independent variables were significantly correlated with recruitment of Lahontan sagebrush. However, multiple stepwise regressions showed July PDO explained the greatest amount of variation in both locations. Specifically, percent recruitment increased with the positive phase of PDO. The Wild Oat Mountain study site is on lithic soils and the soils at Antelope Flat study site are shallow to a duripan with a Xeric moisture regime. These particularly harsh edaphic environments may override contributing climatic factors, contributing to the low $R^2$ value. Low sagebrush and Lahontan sagebrush are closely related subspecies and the positive phase of PDO explained the greatest amount of variation in both.

Some of the relationships explained by the regression analysis have weak descriptive power, but do add to the overall ability to explain recruitment pulses. Weak correlation can be attributed to the wide ecological amplitude occupied by sagebrush,
lack of detailed, real-time climate data and unknown interactions between abiotic factors, biotic factors and plants. Limited correlations can also be attributed to random spatial variability of rainfall, runoff redistribution and edaphic diversity (Noy-Meir 1973). Relatively low $R^2$ values are also a product of the regression analysis. Each stepwise regression for a regional combination included 13 weather related variables, each with a unique value for each year. On average regional stand combinations covered a period of 40 years. The total amount of variation accounted for at a given study site is spread across 520 variables, decreasing the significance of individual variables on a regional level. Variation within and interactions between long term precipitation, elevation, landscape position and various other environmental factors are responsible for the large amount of variation sagebrush species display. Lack of significant correlation between environmental factors and differences within the sagebrush ecosystem have been attributed to interactions on a much finer scale (Davies et al. 2007).

**CONCLUSIONS**

Large scale climate patterns, such as the positive phase of the PDO index, contribute to successful regeneration in stands of sagebrush. The PDO index has been attributed to variation in other terrestrial plant communities. Regeneration in stands of quaking aspen (*Populus tremuliodes*) in the 1970’s coincide with a shift in the PDO index (Kaye 2011). The positive phase of PDO in the 1970’s and 1980’s caused a transition toward wetter growing conditions, resulting in increased aspen regeration (Kaye 2011). Researchers have also found signatures of the PDO index in annual growth rings of
mountain hemlock (*Tsuga mertensiana*), Jeffrey pine (*Pinus jeffreyi*) and bigcone Douglas-fir (*Pseudotsuga macrocarpa*). These dendrochronological records from the western U.S. have extended the PDO index back to the 1600’s (Gedalof and Mantua 2002).

In Nevada, it is imperative that successful methods of seeding sagebrush are established in order to reverse the transition toward annual grasslands dominated by cheatgrass (*Bromus tectorum*). Restoration efforts that are timed correctly with respect to temperature and precipitation will be much more successful and preserve valuable monetary resources. The relationships identified by this study provide insight into the natural life cycle of several species and subspecies of sagebrush. Modern trends in restoration ecology are interested in developing better predictive tools and broad conceptual framework behind the restoration of arid and semi-arid rangelands (Suding et al. 2004). This indicates that an understanding of ecological resistance or resilience of ecosystems, especially degraded or alternative stable states could improve restoration practicies. Invasive species influence biotic factors including biogeochemical cycling, loss of habitat connectivity, and loss of native seed source, all of which influence restoration (Suding et al 2004). Understanding the biotic feedbacks that keep the degraded state stable are essential to understanding how restoration attempts result. Timing restoration attempts with abiotic inputs such as weather, as this research suggests, will reduce the effect of some positive feedbacks existing in the alternative stable state and increase successful restoration attempts. A State-and-Transition Model (STM) for the
Wyoming big sagebrush type provides specific examples of where the findings of this research can be applied in management (Figure 11).

STM’s are conceptual frameworks used to describe vegetation dynamics on rangelands. They include continuous and reversible and discontinuous and non-reversible vegetation dynamics. An important aspect of STM’s is that they provide a link between theoretical expectation and management response (Bestelmeyer et al. 2003). The State-and-Transition concept is designed to provide a method for anticipating departures from a stable state as a plant community nears a threshold and incorporates this understanding into management plans (Bestelmeyer et al. 2003).

STM’s include a Reference State. This state is representative of rangeland plant communities prior to European settlement and plant community dynamics are primarily driven by natural perturbations such as infrequent wildfire and drought. Plant communities can also exist in alternative stable states. Transitions to alternative stable states occur when irreversible biotic or abiotic thresholds are crossed. Plant community phase changes in alternative stable states are the result of disturbances natural or anthropogenic, including wildfire, grazing, droughts, floods and the presence of non-native species.

In the example provided (Figure 11) State 2, State 3, and State 4 are alternative stable states which exist after thresholds are crossed by transitions T1, T2A, T2B and T3 (Figure 11). Transitions represent an invisible threshold or barrier that has been crossed.
Habitat connectivity and seed source are some of these barriers. Rangeland seedings are a type of restoration pathway aimed at addressing these barriers. However, if seedings are not carefully timed, other barriers such as competition and lack of available resources prevent recruitment and establishment of seeded species. Barriers can be influenced by natural factors like frequency of wet or dry years. Conclusions from this research suggest, when rangeland seedings will be used to bring plant communities back to a more desirable state, seedings should be executed in conjunction with predictable variations in climate. Restoration pathways 3 and 4 (Figure 11) provide an illustration of where these management recommendations can be implemented. These revised techniques could result in improved sagebrush establishment and survival on rangelands.

The importance of timing sagebrush seedings with predictable variations in climate is suggested by the significant correlation between natural sagebrush recruitment and PDO index. The PDO index has a long-term predictable influence on North American weather patterns. Mantua et al (1997) found evidence for full PDO cycles during the past century, cool or negative PDO cycles from 1890-1924 and 1947-1976 and warm or positive cycles from 1925-1946 and from 1977 through about the mid-1990’s (Figure 12). The regime shift in 1925, 1947, and 1977 are a distinct characteristic of the PDO index (Mantua 1999). In general the shift from cool to warm phase of the PDO corresponded with increased sagebrush cohort recruitment (Figure 13, 14, 15 & 16).
Warm spring and summer temperatures with adequate soil moisture allow seedlings to achieve a rapid growth rate extending their roots deeper into the soil profile, therefore being able to extract moisture from deeper in the soil profile, increasing chances for survival through the growing season. However, higher monthly temperatures resulting in faster growth rates will deplete soil moisture faster, resulting in a greater desiccation of seedlings. Warm phases of the PDO are characterized by above-average winter and spring precipitation in southern U.S. and northern Mexico (Mantua 1999). It also corresponds with an increased likelihood of extreme precipitation events over southern North America, especially during the winter season (Zhang et al. 2010).

In places where the abundance of non-native annual biomass serves as a barrier to restoration efforts (State 4 Figure 10) other forms of management must be employed to improve success of restoration efforts. For example, grazing non-native annual grasses with cattle or sheep late in the growing season will effectively reduce the competition and threat of wildfire (R4 Figure 10). This type of directed management serves as a disruption that sends the system in a direction that facilitates transition to a desired state (Suding et al. 2004). Degraded sagebrush systems are possible to restore, however, it may not be practical to assume introducing the historic disturbance regime is the only/best way to achieve the final goal. The findings of this research indicate it may be more practical to mimic patterns of recruitment in nature.
Landscape connectivity in the sagebrush ecosystem is threatened by wildfire and invasive species, both of which limit the availability of local seed sources. Seeding native species on rangelands attempts to remedy this issue. Recovery of sagebrush is important for the greater sage-grouse (*Centrocercus urophasianus*). Woody sagebrush species are a major food source and provide critical habitat for the sagegrouse (Rosentreter 2005). Alternative stable states (State 3 & State 4 Figure 9) do not provide habitat of value to sagebrush obligates like the sagegrouse. Recommendations from this research will improve the rate of seeding success and help limit habitat loss and fragmentations issues (R3 & R4 Figure 9).

Maintaining healthy sagebrush ecosystems is important for a variety of ecosystem services including wildlife habitat, aesthetic enjoyment, soil stability and biodiversity. This research provides evidence of factors influencing recruitment patterns in nature and demonstrates where changes to current restoration techniques can be made. Restoration and reclamation success benefits livestock producers, the wildlife community, bird watchers and overall ecosystem health. This research highlighted gaps in our current restoration potential. This is largely a factor of the overall lack of information about the low sagebrush type and minimal information available on the big sagebrush type. Even though this system is widespread and the importance is well known, there is a lack of ecological research specifically about sagebrush. The long-term economic benefits from grasses and trees have excluded shrub research. However,
shrub-dominated arid systems occur around the world and knowledge of their importance will prompt increased research in the future.
Literature Cited


PDO index (http://jisao.washington.edu/pdo/PDO.latest)


<table>
<thead>
<tr>
<th>Species:</th>
<th>Location:</th>
<th>Ecological Site:</th>
<th>Soil Series Name:</th>
<th>Classification of Soil Series:</th>
<th>Soil Characteristics:</th>
<th>Fire return interval:</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. nova (ARNO4)</td>
<td>Spring Valley (SV)</td>
<td>Shallow Calcareous Loam</td>
<td>Ursine</td>
<td>Loamy-skeletal, carbonatic, mesic, shallow Xeric HaploDurid</td>
<td>Shallow to a duripan, well drained, formed in alluvium derived mainly from limestone. Found on fan remnants.</td>
<td>75–290 years</td>
</tr>
<tr>
<td></td>
<td></td>
<td>8-10&quot; P.Z.</td>
<td></td>
<td></td>
<td></td>
<td>(Fryer 2009)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(028AY013NV)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A. nova (ARNO4)</td>
<td>Red Peak (RP)</td>
<td>Shallow Calcareous Loam</td>
<td>Zadvar</td>
<td>Loamy, mixed, superactive, mesic, shallow Haploxeraltic Argidurid</td>
<td>Well drained, shallow to a duripan, derived from volcanic sources. Found on fan remnants.</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>8-12&quot; P.Z.</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>(029XY008NV)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A. tridentata wyomingensis (ARTRW)</td>
<td>Antelope Valley (AV)</td>
<td>Shallow Loam 8-10&quot; P.Z.</td>
<td>Zafod</td>
<td>Loamy skeletal, mixed active, mesic Xereptic HaploDurid</td>
<td>Moderately deep to a duripan, well drained, formed in alluvium from mixed sources. Found on fan remnants.</td>
<td>100-200 years</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(028AY017NV)</td>
<td></td>
<td></td>
<td></td>
<td>(Baker 2006)</td>
</tr>
<tr>
<td>A. tridentata wyomingensis (ARTRW)</td>
<td>Santa Rosa Mts. (SR)</td>
<td>Loamy 10-12&quot; P.Z.</td>
<td>Gochea</td>
<td>Fine loamy, mixed, superactive, frigid Argidurid Argixeroll</td>
<td>Very deep, well drained, formed in alluvium and colluviums from mixed sources. Found on fan piedmont remnants.</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>(025XY014NV)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A. arbuscula arbuscula (ARARA)</td>
<td>Willow Creek Ridge (WCR)</td>
<td>Claypan 10-12&quot; P.Z.</td>
<td>Fulstone</td>
<td>Clayey, smectitic, mesic, shallow Abruptic Xeric Argidurids</td>
<td>Shallow to a duripan, well drained formed in alluvium from igneous sources. Found on fan remnants.</td>
<td>75-290 years</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(025XY018NV)</td>
<td></td>
<td></td>
<td></td>
<td>(Fryer 2009)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(023XY017NV)</td>
<td></td>
<td></td>
<td></td>
<td>(Miller and Rose 1999)</td>
</tr>
<tr>
<td>A. arbuscula longicaulis (ARARL3)</td>
<td>Antelope Flat (AF)</td>
<td>Gravelly Clay 10-12&quot; P.Z.</td>
<td>Fulstone</td>
<td>Clayey, smectitic, mesic, shallow Abruptic Xeric Argidurids</td>
<td>Well drained soils, shallow to a duripan, formed in alluvium from igneous sources. Found on fan remnants.</td>
<td>75-290 years</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(023XY093NV)</td>
<td></td>
<td></td>
<td></td>
<td>(Fryer 2009)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(026XY041NV)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 1: The ecological site, soil series and soil classification information of each study site. (Web Soil Survey)
<table>
<thead>
<tr>
<th>Location</th>
<th>Species</th>
<th>Elevation &amp; Slope</th>
<th>Average annual precipitation</th>
<th>Soil Moisture Regime</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spring Valley (SV)</td>
<td>A. nova (ARNO4)</td>
<td>1849 m (6068 ft)</td>
<td>228 mm (9 inches)</td>
<td>Xeric</td>
</tr>
<tr>
<td>Red Peak (RP)</td>
<td>A. nova (ARNO4)</td>
<td>1936 m (6350 ft)</td>
<td>254 mm (10 inches)</td>
<td>Aridic → Xeric</td>
</tr>
<tr>
<td>Antelope Valley (AV)</td>
<td>A. tridentata wyomingensis (ARTRW)</td>
<td>1795 m (5890 ft)</td>
<td>254 mm (10 inches)</td>
<td>Aridic → Xeric</td>
</tr>
<tr>
<td>Santa Rosa Mountains (SR)</td>
<td>A. tridentata wyomingensis (ARTRW)</td>
<td>1830 m (6005 ft)</td>
<td>305 mm (12 inches)</td>
<td>Aridic → Xeric</td>
</tr>
<tr>
<td>Willow Creek Ridge (WCR)</td>
<td>A. arbuscula arbuscula (ARARA)</td>
<td>1828 m (5997 ft)</td>
<td>305 mm (12 inches)</td>
<td>Xeric</td>
</tr>
<tr>
<td>Montana Mountains (MM)</td>
<td>A. arbuscula arbuscula (ARARA)</td>
<td>1981 m (6499 ft)</td>
<td>356 mm (14 inches)</td>
<td>Aridic</td>
</tr>
<tr>
<td>Antelope Flat (AF)</td>
<td>A. arbuscula longicaulis (ARARL3)</td>
<td>1828 m (5997 ft)</td>
<td>330 mm (13 inches)</td>
<td>Xeric</td>
</tr>
<tr>
<td>Wild Oat Mountain (OM)</td>
<td>A. arbuscula longicaulis (ARARL3)</td>
<td>1584 m (5196 ft)</td>
<td>228 mm (9 inches)</td>
<td>Aridic → Xeric</td>
</tr>
</tbody>
</table>

Table 2: Topographic and climatic characteristics of each study site.
### SUMMARY

<table>
<thead>
<tr>
<th>SPECIES</th>
<th>SITE</th>
<th>COUNT</th>
<th>MEAN AGE</th>
<th>ST ERROR</th>
</tr>
</thead>
<tbody>
<tr>
<td>ARARA</td>
<td>MM</td>
<td>206</td>
<td>18.267</td>
<td>0.6544</td>
</tr>
<tr>
<td></td>
<td>WCR</td>
<td>204</td>
<td>19.294</td>
<td>0.6576</td>
</tr>
<tr>
<td>ARARL3</td>
<td>OM</td>
<td>144</td>
<td>20.319</td>
<td>0.7826</td>
</tr>
<tr>
<td></td>
<td>AF</td>
<td>226</td>
<td>19.708</td>
<td>0.6247</td>
</tr>
<tr>
<td>ARNO4</td>
<td>SV</td>
<td>142</td>
<td>24.944</td>
<td>0.7881</td>
</tr>
<tr>
<td></td>
<td>RP</td>
<td>195</td>
<td>27.185</td>
<td>0.6726</td>
</tr>
<tr>
<td>ARTRW</td>
<td>SV</td>
<td>191</td>
<td>26.597</td>
<td>0.6796</td>
</tr>
<tr>
<td></td>
<td>SR</td>
<td>184</td>
<td>20.592</td>
<td>0.6924</td>
</tr>
</tbody>
</table>

### ANOVA

<table>
<thead>
<tr>
<th>Source of Variation</th>
<th>SS</th>
<th>df</th>
<th>MS</th>
<th>F RATIO</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>SPECIES</td>
<td>12014.464</td>
<td>3</td>
<td>4004.821</td>
<td>45.4036</td>
<td>&lt;.001*</td>
</tr>
<tr>
<td>SITE[SPECIES]</td>
<td>3932.5</td>
<td>4</td>
<td>983.125</td>
<td>11.1459</td>
<td>&lt;.001*</td>
</tr>
</tbody>
</table>

Table 3: A) Summary data of counts and ages for each species and site and B) ANOVA testing for differences between species and sites.
<table>
<thead>
<tr>
<th>SPECIES STUDY SITE</th>
<th>ARNO4</th>
<th>ARARA</th>
<th>ARARL3</th>
<th>ARTRW</th>
</tr>
</thead>
<tbody>
<tr>
<td>MARCH, APRIL MAY</td>
<td>0.0836</td>
<td>0.004</td>
<td>0.0045</td>
<td>0.0478</td>
</tr>
<tr>
<td>JUNE, JULY, AUG</td>
<td>0.0686</td>
<td>0.0026</td>
<td>0.0144</td>
<td>0.0001</td>
</tr>
<tr>
<td>SEPT, OCT, NOV</td>
<td>0.0353</td>
<td>0.0002</td>
<td>0.0006</td>
<td>0.0221</td>
</tr>
<tr>
<td>DEC, JAN, FEB</td>
<td>0.0689</td>
<td>0.0502</td>
<td>0.0127</td>
<td>0.0023</td>
</tr>
<tr>
<td>TOTAL ANNUAL PRECIP</td>
<td>0.2627</td>
<td>0.0085</td>
<td>0.0028</td>
<td>0.0064</td>
</tr>
<tr>
<td>PREVIOUS YEAR PRECIP</td>
<td>0.2558</td>
<td>0.0018</td>
<td>0.0013</td>
<td>0.0092</td>
</tr>
<tr>
<td>FOLLOWING YEAR PRECIP</td>
<td>0.2628</td>
<td>0.0003</td>
<td>0.0055</td>
<td>0.0001</td>
</tr>
<tr>
<td>AVERAGE ANNUAL DEWPOINT</td>
<td>0.0711</td>
<td>0.0356</td>
<td>0.0544</td>
<td>0.1079</td>
</tr>
<tr>
<td>PDO VARIABLES</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>JAN PDO</td>
<td>0.006</td>
<td>0.017</td>
<td>0.001</td>
<td>0.062</td>
</tr>
<tr>
<td>APRIL PDO</td>
<td>0.013</td>
<td>0.064</td>
<td>0.056</td>
<td>0.176*</td>
</tr>
<tr>
<td>JULY PDO</td>
<td>&lt;0.001</td>
<td>0.005</td>
<td>0.106*</td>
<td>0.219*</td>
</tr>
<tr>
<td>SEPT PDO</td>
<td>&lt;0.001</td>
<td>0.032</td>
<td>0.031</td>
<td>0.075</td>
</tr>
<tr>
<td>NOV PDO</td>
<td>&lt;0.001</td>
<td>0.005</td>
<td>0.007</td>
<td>0.002</td>
</tr>
<tr>
<td>RESULTS</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>STEPWISE FIT with PDO</td>
<td>0.5176</td>
<td>0.285</td>
<td>0.1058</td>
<td>0.3669</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 4. Species, subspecies, regional and stand $R^2$ values from stepwise regression analysis. Significant individual $R^2$ values denoted with an asterisk.
Figure 1: Nevada map with study site locations

LEGEND

Study site code and name
- AF = Antelope Flat (ARARL3)
- OM = Oat Mountain (ARARL3)
- MM = Montana Mountains (ARARA)
- WCR = Willow Creek Ridge (ARARA)
- SR = Santa Rosa Mountains (ARTRW)
- AV = Antelope Valley (ARTRW)
- SV = Spring Valley (ARNO4)
- RP = Red Peak (ARNO4)

Species/subspecies code and name
- ARARL3 = A. arbuscula spp. longicaulis
- ARARA = A. arbuscula spp. arbuscula
- ARTRW = A. tridentata spp. wyomingensis
- ARNO4 = A. nova
Figure 2: Map of total annual precipitation in Nevada with MLRA boundaries.
Figure 3: Maximum, mean and minimum stand age for each species and site. Species and site code found in Table 1 and 2.
Figure 4: Negative distribution recruitment frequency plots with standard error bars and quantile box plots for each species and site. Quantile box plot shows smallest observation, lower quantile (25%), meadian (50%), upper quantile (75%), largest observation and the mean confidence diamond. The mean confidence diamond indicated the sample mean and 95% confidence interval.
Figure 5: Mean age by species. **A, B & C indicate statistically significant differences in species mean age.

Figure 6: Mean age by species and site.
Figure 7: *A. arbuscula* spp. *longicaulis* regional stand age frequency distribution.

Figure 8: *A. nova* regional stand age frequency distribution.
Figure 9: *A. tridentata* spp. *wyomingensis* regional stand age frequency distribution

Figure 10: *A. arbuscula* spp. *arbuscula* regional stand age frequency distribution.
Wyoming big sagebrush draft STM

State 1: Reference State
Plant Community 1.1
Wyoming big sagebrush dominant. Perennial bunchgrasses dominant in understory.

State 2: Invaded State
Similar to Reference State with non-natives in the understory. Perennial bunchgrasses and forbs present.
Decreasing perennial bunchgrasses. Increasing non-natives and bare ground.

State 3: Shrub State
Sagebrush over dominant and decadent with little recruitment. Perennial grasses decreasing. Non-natives and bare ground increasing.
Sagebrush and other shrubs over dominant. Few perennial grasses. Reduced infiltration, risk of soil erosion significant.

State 4: Annual State
Non-native annuals dominant. Risk of soil erosion significant.
Disturbance tolerant shrubs increase. Non-native annuals dominate understory. Bare ground increases. Sagebrush absent.

LEGEND
• T1 (Transition 1): Introduction of non-native species
• T2A (Transition 2A): Abusive grazing or prolonged drought
• T2B (Transition 2B): Frequent and repeated wildfire
• R3 (Restoration Pathway 3): Seed native species timed with predictable variations in climate. Herbicide to control non-natives
• T3 (Transition 3): Frequent and repeated catastrophic wildfire
• R4 (Restoration Pathway 4): Seed native species timed with predictable variations in climate. Possibly use prescribed grazing to control fuel loading

Figure 11: Example STM with restoration recommendations
Figure 12: Sliding 5 years average of January, April, July, September, and November PDO index values.

Figure 13: *A. arbuscula* spp. *longicaulis* regional stand age frequency distribution with yearly PDO index
Figure 14: *A. tridentata* spp. *wyomingensis* regional stand age frequency distribution with yearly PDO index

Figure 15: *A. nova* regional stand age frequency distribution with yearly PDO index
Figure 16: *A. arbuscula* spp. *arbuscula* regional stand age frequency distribution with yearly PDO index