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Original Research

Climatic Influences on Establishment Pulses of Four *Artemisia* Species in Nevada[☆]

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ABSTRACT

Shrub recruitment in arid and semiarid regions often occurs in pulses controlled by specific weather events. Previous research suggested that Wyoming sagebrush in Wyoming is no exception. We examined four species/subspecies of sagebrush in Nevada, in 2009 and 2010, to discover if evidence of recruitment pulses was contained in the annual growth-ring records. Sagebrush species and subspecies occur on a wide variety of ecological sites that require different management strategies. Species included black sagebrush (*Artemisia nova* A. Nelson), Wyoming big sagebrush (*Artemisia tridentata* subsp. *wyomingensis* Beetle & Young), Lahontan sagebrush (*Artemisia arbuscula* subsp. *longicaulis* Winward & McArthur), and low sagebrush (*Artemisia arbuscula* Nutt. ssp. *arbuscula*). Eighty stem sections were collected from each of 24 stands (6 stands per species or subspecies) at different geographic locations along east-west or north-south gradients where each species or subspecies naturally occurred. Annual growth-ring analysis was used to determine the year of establishment and the relationship between recruitment and weather events. Results indicated stand ages and locations were different ($P > 0.001$) among species and subspecies, and years of recruitment were strongly correlated with local and hemispheric weather patterns. Linear and multiple regressions modeled recruitment pulses for all four species. Weather-based predictor variables indicated complex interactions between recruitment and climatic controls. Pacific Decadal Oscillation (PDO) index variables were prominent predictors for all four species at their associated sites. Other important local weather variables included total annual precipitation the year before recruitment, the year of recruitment, and the year following recruitment. In Nevada and the Great Basin, it is imperative that successful sagebrush seeding technologies are discovered and implemented. Ecological restoration and postfire rehabilitation methods should be timed correctly with respect to precipitation patterns (positive phase PDO) and/or designed to mimic conditions responsible for natural sagebrush recruitment.

Introduction

Woody sagebrush species (*Artemisia* L. spp.) occurrence is circumpolar and often vitally important to the ecological stability and function of the ecosystems they populate. Species from the section *Tridentatae* of the genus *Artemisia* are probably the most spatially widespread shrub (geographic and elevation) in western North America (Meyer, 2008). In the Intermountain West, most members of the section are found on well-drained soils, typically *Aridisols* or *Mollisols,* in areas with relatively cold winters. Annual precipitation is generally low (200 – 700 mm) and occurs largely during the winter months (Beetle and Johnson, 1982). *Artemisia* (L.) is the dominant genus throughout much of the Columbia and Colorado Plateaus, the Great Basin, and western Wyoming. The North American fossil record and later historical accounts indicate that sagebrush has existed in its approximate present-day distribution for at least 1.2 million yr (Tidwell et al., 1972; Barnosky et al., 1987).

Information about sagebrush germination requirements is limited to a few species. Evidence suggests that sagebrush seed requires both cold and light stratification to eliminate dormancy (Meyer, 2008). The amount of precipitation occurring from March to November is a good predictor of sagebrush seed weight (Busso and Perryman, 2005), and greater seed weight is positively correlated with better germination percentages (Busso et al., 2005). Germination timing mechanisms and successful establishment are keyed to a pattern of winter or early spring germination and early spring emergence, for all of the species previously examined (Meyer, 2008). The timing of germination is strongly related to weather variables at the seed collection site (Meyer, 2008). For example, seeds from high-montane environments with long, cold, snowy winters tend to germinate later (i.e., resist early germination),

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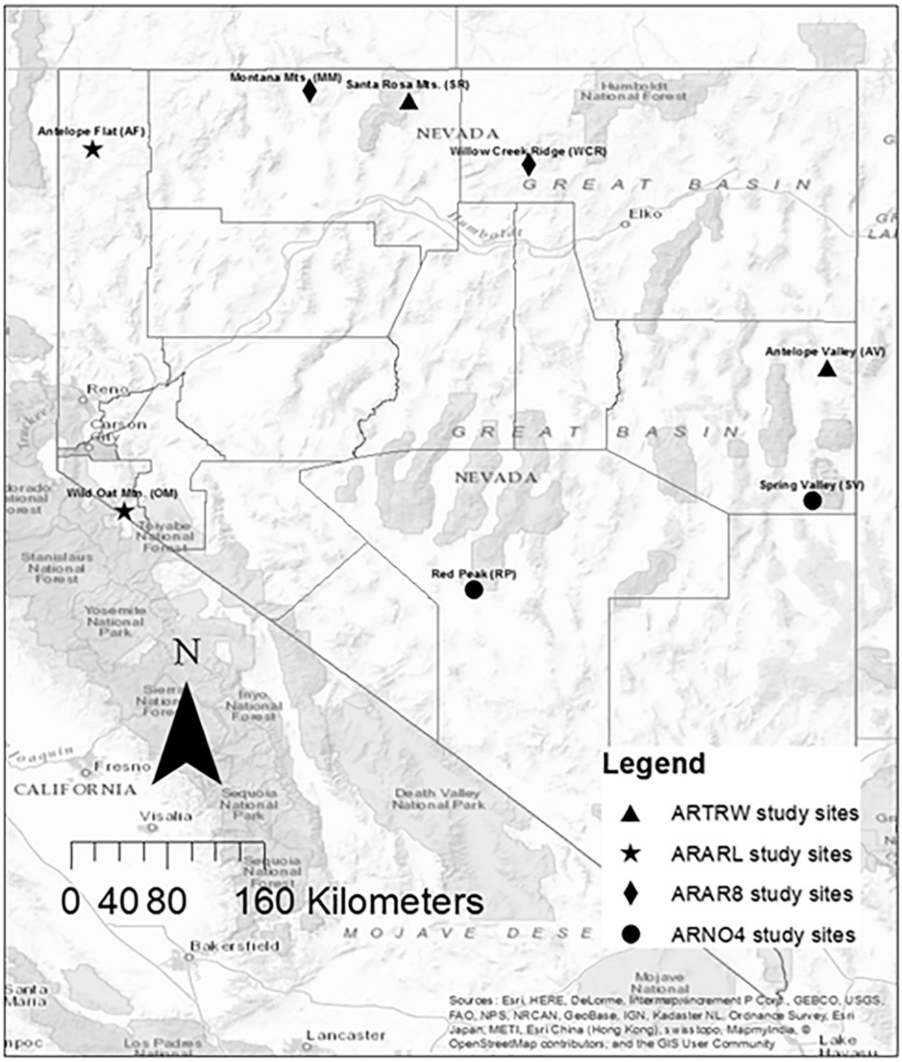

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Figure 1. Study site locations.

which protects seeds and their embryos from emerging before temperature conditions are optimum for seedling survival.

Irregular, climatically controlled demographic pulses have been demonstrated for sagebrush species in Wyoming and British Columbia (Cawker, 1980; Perryman et al., 2001) but have not been studied in Nevada. Maier et al. (2001) hypothesized that in northeastern Wyoming, persistent winter snow cover served to protect seedlings from winter desiccation while providing additional soil moisture during snowmelt, ultimately controlling the magnitude of the demographic pulse. Snow cover in Nevada, especially at lower elevations (< 1 829 m) is often less seasonally persistent than in Wyoming.

Several researchers have delineated the presence of climatically controlled demographic pulses in sagebrush and other shrub species across the western United States (West et al., 1979; Cawker, 1980; Maier et al., 2001; Perryman et al., 2001). Understanding the climatic controls responsible for major demographic pulses of various sagebrush species can provide information about cultural practices that may increase the efficiency and success of ecological restoration or fire rehabilitation projects. Knowledge about demographic pulses will also improve our understanding of plant community dynamics, resulting in better state-and-transition models and land management plans. For example, the frequency and size of recruitment pulse events (Maier et al., 2001; Perryman et al., 2001) determines the time needed for an intact sagebrush site that has lost its sagebrush canopy but retains its perennial bunchgrasses to return to its previous level of sagebrush site occupancy. Furthermore, the time required for a return to a previous level of site occupancy is likely to vary by sagebrush species or subspecies and perhaps geographic location in the Great Basin. Since different sagebrush species/subspecies occur on different ecological sites that may require different rehabilitation techniques, several widespread species of sagebrush require investigation. The objectives of this study were to 1) investigate the demographic characteristics of four widespread sagebrush species important to Nevada ecosystems including black sagebrush (*Artemisia nova* A. Nelson), Wyoming big sagebrush (*Artemisia tridentata* subsp. *wyomingensis* Beetle & Young), Lahontan sagebrush (*Artemisia arbuscula* subsp. *longicaulis* Winward & McArthur), and low sagebrush (*Artemisia arbuscula* Nutt.); and 2) determine how demographic characteristics are affected by weather variables or trends in annual precipitation.

Methods

In early 2009, study sites (Fig. 1) that represented different locations along geographic gradients where the species or subspecies of interest occurred in unseeded stands were identified. Individual stands were chosen for analysis if they appeared to have multiple cohorts; were similar in ecological site and landscape position; and were relatively free from disturbance (e.g., recent wildfire; obvious insect infestations; or excessive grazing by feral horses, wildlife, or domestic livestock). The promiscuous nature of the *Artemisia* (L.) genus (Beetle, 1960) also required avoiding areas that were near other sagebrush species, reducing the influence of hybridization and/or ecotones. Species and subspecies were identified using botanical keys, technical notes, and special publications (Beetle, 1960; Plummer, 1986; Winward and McArthur, 1995; Schultz and McAdoo, 2002; Rosentreter, 2005; Shultz, 2007).

For each species or subspecies, 80 stem cross-sections were collected (Cawker, 1980; Maier et al., 2001) from each of three stands on two sites that represented an east-west or north-south gradient. This resulted in 24 stands and 1 920 total stem sections (6 stands × 4 species/subspecies × 80 individual plants). Black sagebrush stem sections were collected from Spring Valley (SP, near Ely, Nevada) and Red Peak (RP, near Tonopah, Nevada), an east-west gradient. Elevation ranged from 1 849 to 1 936 m, with an average annual precipitation range of 228 − 254 mm. Wyoming big sagebrush was collected from Antelope Valley (AV, near Tippet Pass) and the Santa Rosa Mountains (SR, near Winnemucca, Nevada), a northwest-southeast gradient. Elevation ranged from 1 795 to 1 830 m, with an average annual precipitation range of 254 − 305 mm. Lahontan sagebrush was collected from Antelope Flat (AF, near Vya, Nevada) and on Wild Oat Mountain (OM, near Topaz Lake, Nevada), a north-south gradient. Elevation ranged from 1 584 to 1 828 m, with an annual average precipitation of 228 − 330 mm. Low sagebrush was collected on Willow Creek Ridge (WCR, near Midas, Nevada) and from the Montana Mountains (MM, near Orovada, Nevada), an east-west gradient. Elevations ranged from 1 828 to 1 981 m with an average annual precipitation of 305 − 356 mm. GPS coordinates, soil series, and ecological site information for each stand are shown in Table 1.

A stratified-random sampling method was used to select plants for stem cross-sections from each stand (Roughton, 1972). A 100-m long baseline transect was located within each stand, and ten 100-m long perpendicular transects were established at randomly selected points along the baseline. Along each perpendicular transect, eight random points were selected and the closest individual sagebrush plant that met the sampling criteria was collected ($n = 80$). Sampling of individual plants was limited to those with intact main stems. When a usable plant was identified, the stem cross-section was obtained by cutting the plant off below the root crown to ensure that the pith and the first annual growth-ring were included (Ferguson, 1964). For this study we had to obtain a complete record of annual growth-rings to determine the year of establishment. For many species of sagebrush with a short and somewhat spreading growth form, older plants often lack radial stem symmetry. Over time, the accumulation of soil and organic matter at the root crown results in stem splitting and rotting, as well as the loss of the early annual growth-rings. We eliminated these plants from sampling; thus, our sampling method was biased toward single-stem plants with intact growth-rings and pith. This often resulted in excluding the oldest individuals and biasing demography curves toward younger individuals and cohorts.

Samples were then taken to the laboratory and prepared for annual growth-ring analysis. After sawing to expose the pith at the junction of the root crown and stem, cross-sections were sanded with progressively finer grit sand paper (120-220-320 grit) on an electric belt sander (Ferguson, 1964). Annual growth-rings were examined using a 10-power stereomicroscope and enumerated once by two individuals for a total of two observations per sample (Perryman et al., 2001). Annual growth-rings in sagebrush species can be difficult to count because growth throughout the cross section is often not concentric. Stem-sections easily decay in the center, split along the side, and can have growth lobes on only one side of the stem. The first annual growth-ring and pith are visible due to its characteristically light color and small size. When the two initial observations disagreed on the stem-section age, it was resanded with progressively finer sandpaper and counted a third and final time. If both observers did not agree upon the cross-section's age, the sample was rejected. Actual ages were counted from the pith to the live cambium on the perimeter of the cross-section.

Average monthly precipitation values were generated for each site and grouped into quarterly totals representative of each weather season. Precipitation values used in the study included the Parameter-elevation Regressions on Independent Slopes Model (PRISM data) developed by the Spatial Climate Analysis Service at Oregon State University (PRISM, 2004). Generally, there are consistencies in monthly

Table 1

Location, ecological site number, soil series name, soil series classification, and soil profile characteristics at each study site, Nevada, United States, 2011.

Artemisia species	Location	[1]Soil series and ecological site	[1]Soil series classification	[1]Soil characteristics
A. nova (ARNO4)	Spring Valley (SV) [38.7789°°N, 114.3698°W]	Ursine 028AY013NV	Loamy-skeletal, carbonatic, mesic, shallow Xeric Haplodurid	Well drained, 36-51 cm to a duripan, WHC about 4.6 cm, derived in alluvium from limestone. Found on fan remnants.
A. nova (ARNO4)	Red Peak (RP) [38.1167°N, 116.9001°W]	Zadvar 029XY008NV	Loamy, mixed, superactive, mesic, shallow Haploxeraltic Argidurid	Well drained, 25-36 cm to a duripan, WHC about 8.8 cm, derived from volcanic sources. Found on fan remnants.
A. tridentata wyomingensis (ARTRW)	Antelope Valley (AV) [39.7686°N, 114.2588°W]	Zafod 028AY017NV	Loamy skeletal, mixed active, mesic Xereptic Haplodurid	Well drained, 51-99 cm to a duripan, WHC about 4.8 cm, alluvium from mixed sources. Found on fan remnants.
A. tridentata wyomingensis (ARTRW)	Santa Rosa Mts. (SR) [41.7615°N, 117.3742°W]	Gochea 025XY014NV	Fine loamy, mixed, superactive, frigid Argiduridic Argixeroll	Very deep (200 cm), well drained, WHC about 14 cm, formed in alluvium and colluviums from mixed sources. Found on fan piedmont remnants.
A. arbuscula arbuscula (ARARA)	Willow Creek Ridge (WCR) [41.2845°N, 116.4869°W]	Fulstone 025XY018NV	Clayey, smectitic, mesic, shallow Abruptic Xeric Argidurids	Well drained, 36-51 cm to a duripan, WHC about 6 cm, formed in alluvium from mixed and igneous sources. Found on fan remnants.
A. arbuscula arbuscula (ARARA)	Montana Mts. (MM) [41.8344°N, 118.1224°W]	Walti 023XY017NV	Fine, smectitic, frigid Aridic Argixerolls	Well drained, 51-76 cm to bedrock, WHC about 7.4 cm, formed in residuum and colluvium from igneous sources. Found on hills, mountains, and plateaus.
A. arbuscula longicaulis (ARARL3)	Antelope Flat (AF) [41.4041°N, 119.7361°W]	Fulstone 023XY093NV	Clayey, smectitic, mesic, shallow Abruptic Xeric Argidurids	Well-drained soils, shallow to a duripan, formed in alluvium from igneous sources. Found on fan remnants.
A. arbuscula longicaulis (ARARL3)	Wild Oat Mtn. (OM) [38.7066°N, 119.5047°W]	Loomer 026XY041NV	Clayey-skeletal, smectitic, mesic Lithic Argixerolls	Well drained, 36-51 cm to bedrock, WHC about 4.3 cm, formed in colluvium and residuum from igneous sources. Found on hills and mountains.

[1] Designations from Web Soil Survey, 2011, https://websoilsurvey.sc.egov.usda.gov/App/HomePage.htm.

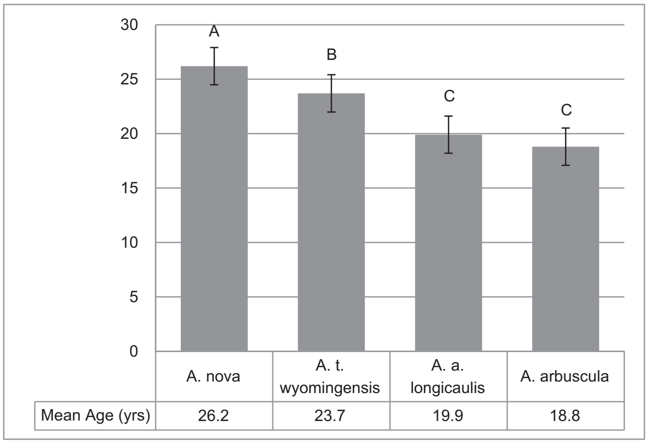

Figure 2. Mean ages (years) and SE bars for four species of sagebrush in Nevada, United States 2011. (Different superscripts denote differences at $P = 0.001$.)

precipitation variables, especially in regions like the Great Basin where winter precipitation is typically greater than summer precipitation (Noy-Meir, 1973). Quarterly groups were chosen to represent soil moisture availability and phenological development of the plant during the year of recruitment. They were 1) spring (March-April-May), 2) summer (June-July-August), 3) fall (September-October-November), and 4) winter (December-January-February). Total annual precipitation variables were generated for the year before recruitment, the year of recruitment, and the year following recruitment. Additional variables analyzed were average annual dewpoint and monthly values from the Pacific Decadal Oscillation (PDO) index. Dewpoint is the temperature to which a parcel of humid air must be cooled for water vapor to condense into liquid water. Dewpoint was hypothesized to be important for seedling recruitment 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 wind stress.

PDO is defined as a long-lived El Nino — like pattern of Pacific climate variability (Mantua, 1999), and like El Nino, PDO influences variability in large-scale climate patterns over North America. However, PDO events persist for 20 — 30 yr while El Niño events typically last for only 6 — 18 months. The climatic signature of PDO is most visible in the North Pacific/North American sector with secondary signatures characteristic in the tropics, but the opposite is true for El Nino (Mantua, 1999). The PDO index is useful in predicting extreme variations in the weather patterns of a particular region, such as droughts or floods (Benson et al., 2003; Zhang et al., 2010). PDO index variables are expressed in positive (warm phase) and negative (cool phase) values. The positive or warm phase includes warmer than normal winter and spring temperatures in the northwest and above-average precipitation in the southwest and northern Mexico. The negative or cool phase is correlated with the opposite.

Statistical Methods

Analysis of variance (ANOVA) was used to compare plant age among species and sites. Linear regression modeled relationships between percent of cohort recruitment in a given year and weather variables. Predictor variables evaluated were monthly temperature variables (maximum, minimum, and mean); quarterly precipitation totals (spring, summer, fall, winter); total precipitation during the year of recruitment, year before recruitment, and year following recruitment; average annual dewpoint; and PDO index values for January, April, July, September, and November. PDO index variables are generally correlated. To correct for multicollinearity, variables with multivariate correlations greater than $r = 0.75$ were not included in the final assessment. Excluded variables were February, March, May, June, August, October, and December PDO.

Stepwise-multiple-regression was used to identify the best combination of weather variables as predictors of *Artemisia* (L.) recruitment, and Student's *t*-test was used to assess the slope of the regression lines. All data were analyzed with JMP Statistical Analysis Software version 7.0.2 (SAS, 2008), and differences were determined at $P < 0.05$ for all analyses.

Results

Demography

Mean ages by species were different among species and by site ($P < 0.001$, Fig. 2). Among all four sagebrush species, black sagebrush stands had a mean age of 26.3 yr, 2.5 — 7.4 yr older than the other three species. Wyoming sagebrush stands had a mean age of 23.7 yr, which was 3.8 and 4.9 yr older than Lahontan sagebrush and low sagebrush, respectively. Mean age of Lahontan sagebrush and low sagebrush stands was 19.9 and 18.8 yr, with no statistical difference.

The comparison of mean stand age between sites within a species or subspecies generally indicated similar ages (Fig. 3). The two Wyoming big sagebrush stands had the greatest difference in mean age, and it was the only within-species mean age comparison that differed statistically. The mean ages of the two black sagebrush stands were within

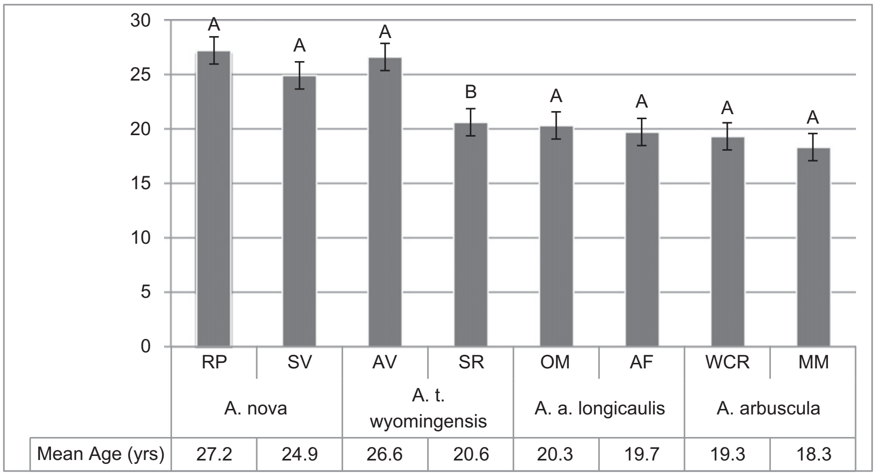

Figure 3. Mean ages (years) and SE bars for four species of sagebrush by stand location (RP, SV, OM, AF, AV, SR, WCR, and MM) in Nevada, United States 2011. (Different superscripts denote differences at $P = 0.001$.)

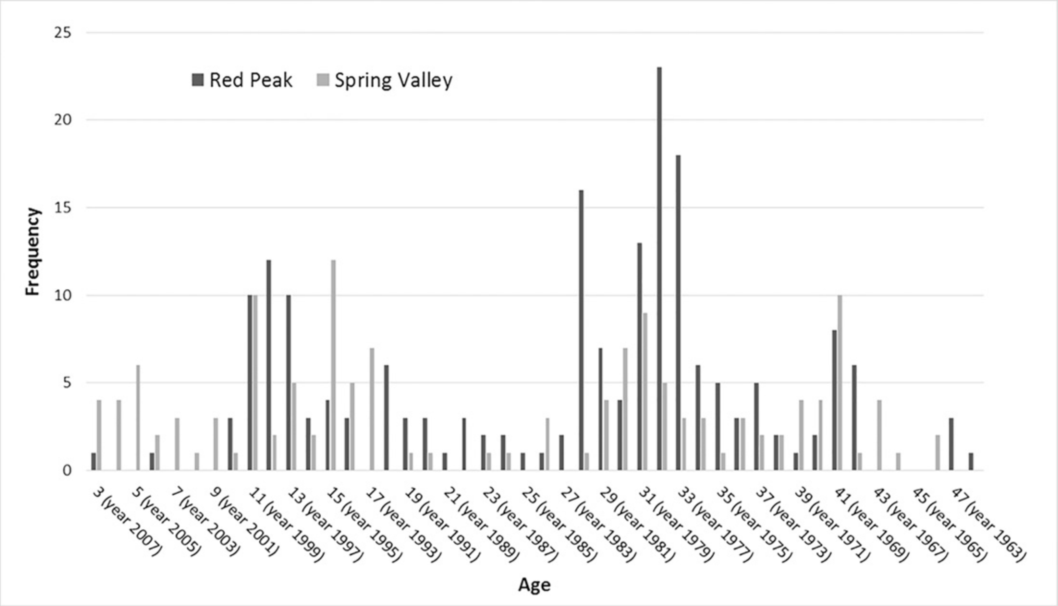

Figure 4. *Artemisia nova* regional stand age frequency distribution, Nevada, United States, 2011.

2.3 yr of one another, and the two stands each of low and Lahontan sagebrush were within about 1 yr of the same mean age.

At the individual level, the oldest black sagebrush plant sampled at the RP site was 77 yr and the youngest 3 yr. This was similar to the age structure at the SV site, where the oldest individual was 73 yr and the youngest was 4 yr. The oldest Wyoming sagebrush plant at the AV site was 79 yr (this was the oldest individual encountered in the study), and the youngest was 2 yr. The maximum age at the SR site was much younger, 40 yr, with the youngest plant a 6-yr-old.

Lahontan and low sagebrush had similar maximum and minimum ages. The oldest individual Lahontan sagebrush plant was found at the OM site and was 57 yr old, while the youngest was 11. The oldest plant at the AF site was 40 yr old, and the youngest was 6. Low sagebrush had the youngest average age of all four species. The oldest low sagebrush plant at the WCR site was 49 yr, and the youngest was 8. A similar age range occurred at the MM site, where the oldest plant was 40 yr and the youngest was 5.

Histograms of stand age frequency distribution show a common recruitment pattern among both species and study sites: periodic large recruitment pulses often interspersed among long periods with little or no recruitment (Figs. 4–7). Demographic analysis indicated that these irregular episodic recruitment pulses follow a negative binomial

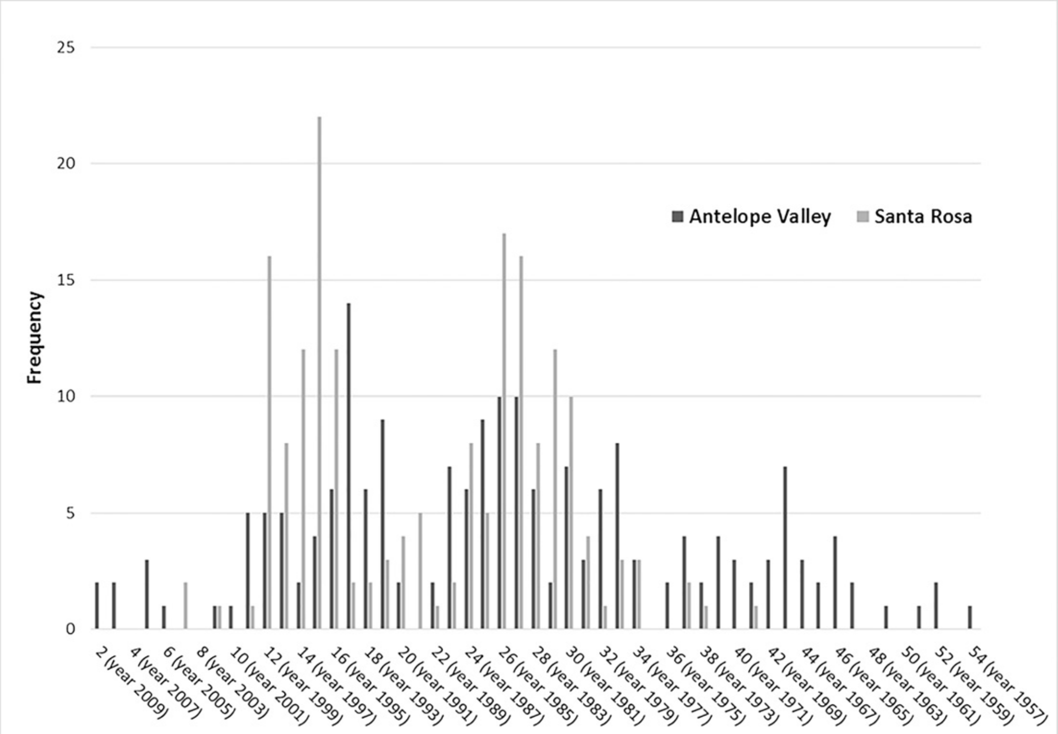

Figure 5. *Artemisia tridentata* subsp. *wyomingensis* regional stand age frequency distribution, Nevada, United States, 2011.

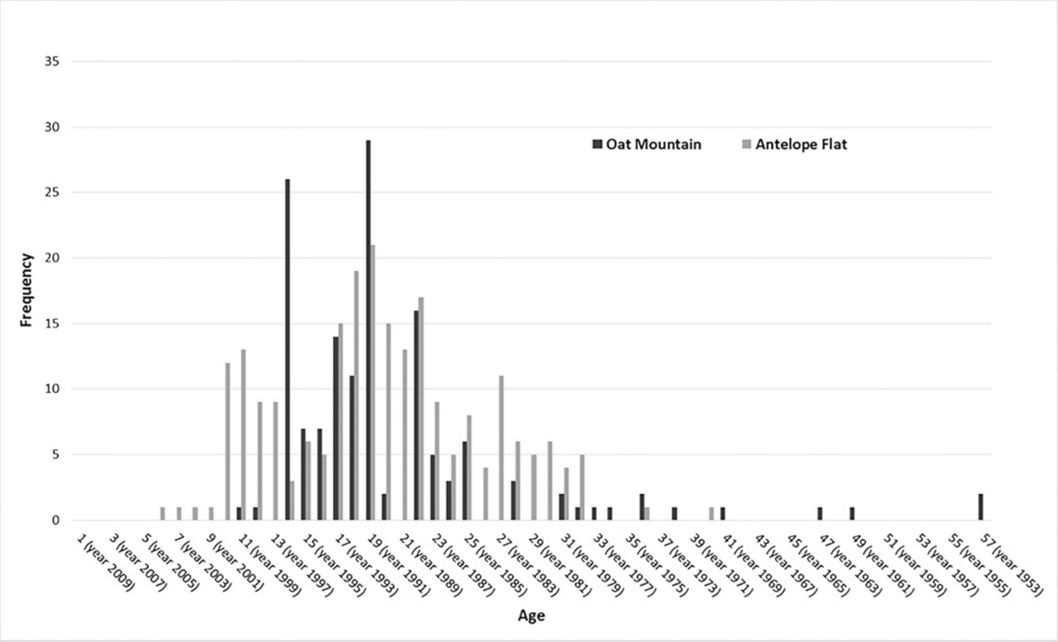

Figure 6. *Artemisia arbuscula* subsp. *longicaulis* regional stand age frequency distribution, Nevada, United States, 2011.

distribution pattern (Fig. 8). The period of record for each species and site was characterized by the majority of yr having little or no recruitment, a moderate number of yr with some recruitment, and only a few yr with relatively high recruitment. For each species, the recruitment pulses did not always occur in the same yr at the two study sites.

Although the periods of record are characterized by a large percentage of yrs with little or no recruitment, yrs with high recruitment were often analogous for individual species and subspecies at different study sites. Black sagebrush at the SV site had its greatest recruitment in 1968, 1994, and 1998, while at the RP site, its best recruitment yrs were 1977, 1978, and 1982. Additional yrs with good recruitment were 1979, 1998, and 1999. It is particularly noteworthy that large pulses occurred at both locations, which are approximately 250 km apart (see Fig. 1), in 1978, 1979, and 1998.

Wyoming sagebrush at the AV site had its best recruitment in 1983, 1984, and 1993, with slightly less recruitment in 1986 and 1992. For the SR site, the best recruitment yrs were in 1984, 1985, 1996, and 1999. Moderate recruitment occurred at both sites in 1981, 1983, 1984, 1985, and 1987. Lahontan sagebrush at the AF and OM sites shared large recruitment pulses in 1988, 1991, 1992, and 1993. Exceptional recruitment pulses occurred twice at Oat Mountain and only once at Antelope Flat.

Large pulses of recruitment occurred for low sagebrush at the WCR site in 1990, 1995, 1997, and 1998. Very high recruitment occurred at the MM site in 1984, 1995, 1996, and in 2004. Most yrs with high recruitment across both sites occurred in the 1980s and 1990s. The exception was 2004 when recruitment was high, but only at the MM site.

Linear Regression Models

Linear regression models (Table 2) indicated that for three of the four sagebrush species, at least one population had recruitment pulses correlated with one or more individual weather variables. Lahontan sagebrush was the exception, having no statistical correlation between recruitment pulses and weather variables. Important weather variables for at least one population of each species included summer quarter

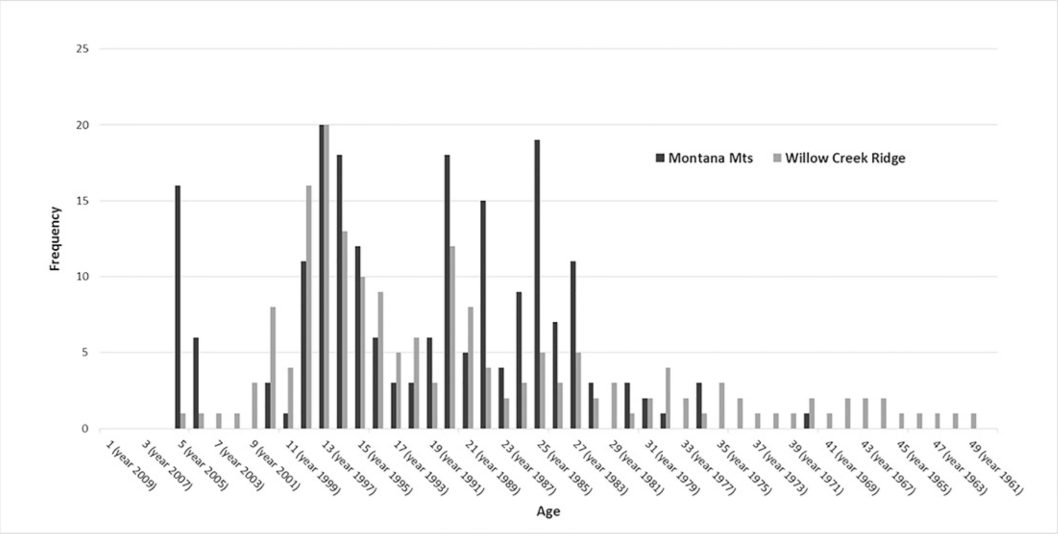

Figure 7. *Artemisia arbuscula* subsp. *arbuscula* regional stand age frequency distribution, Nevada, United States, 2011.

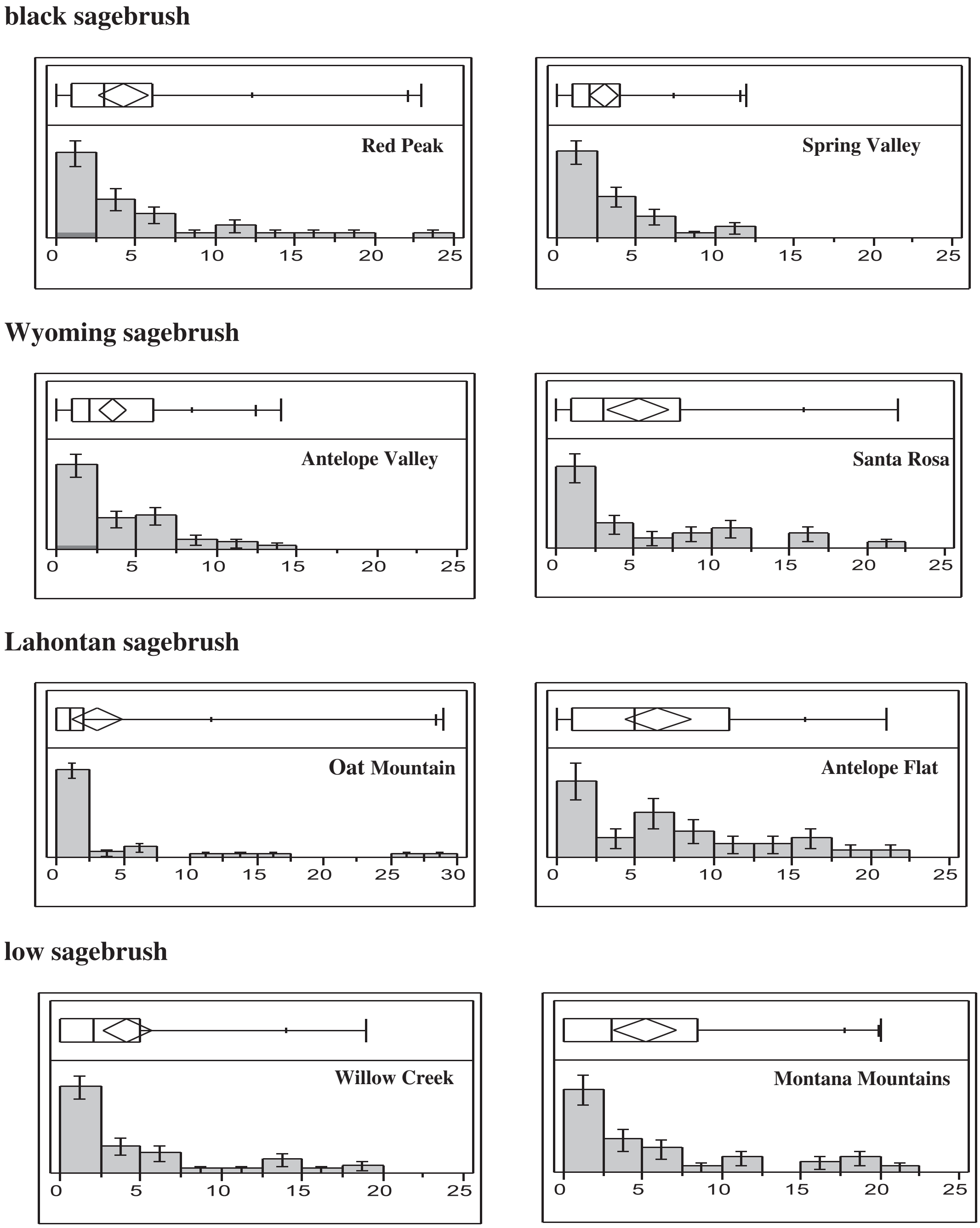

Figure 8. Negative binomial distribution frequency plots with standard error bars and quantile box plots for each species and site. The Y axis is frequency (the number of years with recruitment), and the X axis is the number of individual plants in a recruitment pulse. Quantile box plot shows smallest observation, lower quantile (25%), median (50%), upper quantile (75%), largest observation, and the mean confidence diamond. The mean confidence diamond indicates the sample mean and 95% confidence interval; Nevada, United States, 2011.

precipitation, fall precipitation, total precipitation the yr of recruitment, total precipitation the yr before, and the yr following recruitment, average annual dew point, and PDO indices. Populations and species, however, did not always exhibit similar predictable relationships between recruitment pulses and weather variables. Monthly temperature variables (maximum, minimum, and mean) were poor recruitment predictors and are not presented here. Stepwise-multiple-regression showed that some combinations of weather variables were much better predictors of recruitment pulses than individual weather variables, but there was wide variation among sagebrush species and for populations within species.

For black sagebrush, the largest amount of variance at the RP site for large recruitment pulses was explained by precipitation the year before recruitment ($R^2 = 0.256$), the yr following recruitment ($R^2 = 0.263$), and the total annual precipitation during the yr of recruitment ($R^2 = 0.263$). At the SV site, no variables had significant slopes; however, the two variables with the highest coefficients of determination were December-February precipitation ($R^2 = 0.050$) and the positive phase April PDO index value ($R^2 = 0.064$).

For Wyoming sagebrush, large recruitment pulses at the AV site were significantly correlated with precipitation the year of recruitment ($R^2 = 0.168$), June-August precipitation ($R^2 = 0.096$), and September-November precipitation ($R^2 = 0.1112$). All five PDO variables had significant relationships with recruitment pulses at the AV site as well (see Table 2). At the SR site, precipitation the yr before recruitment

Table 2
Sagebrush species or subspecies and stand R^2 values from simple linear and stepwise-multiple regression analyses, Nevada, United States, 2009.

	Species >	Black sagebrush		Wyoming sagebrush		Low sagebrush		Lahontan sagebrush	
Regression model	Site[1] >	RP	SV	SR	AV	WCR	MM	AF	OM
MAR-MAY[2]		0.084	0.004	0.093	0.014	0.005	0.048	0.025	0.029
JUNE-AUG		0.069	0.003	0.055	0.096*	0.014	<0.001	0.017	0.003
SEPT-NOV		0.035	<0.001	0.016	0.111*	0.001	0.022	0.006	0.002
DEC-FEB		0.069	0.050	0.081	0.019	0.013	0.002	0.059	0.001
PYOR		0.263*	0.009	0.085	0.168*	0.003	0.006	0.002	<0.001
PYPR		0.256*	0.002	0.366*	0.061	0.001	0.009	0.005	0.011
PYFR		0.263*	<0.001	0.038	0.061	0.006	<0.001	0.001	0.007
AADPT		0.071	0.036	0.080	0.021	0.054	0.108*	<0.001	0.050
JAN PDO		0.006	0.017	0.108	0.078*	0.001	0.062	0.032	0.004
APRIL PDO		0.013	0.064	0.143*	0.129*	0.056	0.176*	0.085	0.040
JULY PDO		<0.001	0.005	0.094	0.146*	0.106*	0.219*	0.099	0.066
SEPT PDO		<0.001	0.032	0.043	0.125*	0.031	0.075	0.083	0.044
NOV PDO		<0.001	0.005	0.003	0.080*	0.007	0.002	0.002	0.042
STEPWISE BEST FIT		0.518*	0.285*	0.605*	0.252*	0.106*	0.367*	0.344*	0.0656*

Regressions with significant slopes ($P < 0.05$) denoted with an asterisk.

[1] Site codes: RP = Red Peak; SV = Spring Valley; SR = Santa Rosa; AV = Antelope Valley; WCR = Willow Creek Ridge; MM = Montana Mountains; AF = Antelope Flat; OM = Oat Mountain.

[2] Weather variable code: MAR-MAY, JUNE-AUG, SEPT-NOV, DEC-FEB precipitation; PYOR: precipitation the year of recruitment; PYPR: precipitation the year before recruitment; PYFR: precipitation the year following recruitment; AADPT: average annual dewpoint; PDO: Pacific Decadal Oscillation.

and the April PDO were significant pulse predictors ($R^2 = 0.366$, and 0.143, respectively). All PDO variables at both sites were associated with the positive PDO phase.

For low sagebrush, positive-phase July PDO was the only significant predictor at the WCR site ($R^2 = 0.106$). At the MM site, important predictors were positive phase April ($R^2 = 0.176$) and July PDO ($R^2 = 0.219$) and average annual dewpoint ($R^2 = 0.1079$). None of the individual weather variables had significant slopes for Lahontan sagebrush at either site.

Multiple Regression Models

The best fit stepwise-multiple-regression model (in order of variable strength) for black sagebrush at the RP site ($R^2 = 0.518$) included precipitation the yr following recruitment, precipitation the yr before recruitment, April PDO, and June-August precipitation. At the SV site ($R^2 = 0.285$), predictor variables were April PDO, average annual dewpoint, September PDO, precipitation the yr of recruitment, and July PDO. For Wyoming sagebrush, best fit predictor variables at the AV site ($R^2 = 0.252$) included precipitation the yr of recruitment, July PDO, and December-February precipitation. At the SR Wyoming site ($R^2 = 0.605$), best fit variables were total precipitation the yr before recruitment, April PDO, March-May precipitation, June-August precipitation, July PDO, and January PDO.

For Lahontan sagebrush at the OM site, the only predictor was July PDO ($R^2 = 0.066$). At the AF site ($R^2 = 0.344$), best fit variables included July PDO, December-February precipitation, and April, January, and November PDO. Low sagebrush recruitment at the WCR site was predicted only by July PDO; at the MM site ($R^2 = 0.367$), the best fit model included July PDO, November PDO, average annual dewpoint, and December-February precipitation.

Discussion

Individual plant age and stand ages in this study were generally younger than those found in other sagebrush dendrochronology studies (Ferguson, 1964; Cawker, 1980; Perryman et al., 2001). Our sampling method was limited to single-stem plants with intact growth-rings and pith, systematically excluding older individuals and biasing demography curves toward younger cohorts; however, there was little to no visual evidence of older cohorts or individual shrubs growing at any sites.

Large-scale disturbances including fire, drought, and Aroga moth (*Aroga websteri* Clarke) can decrease the average age of sagebrush stands by causing simultaneous mortality of multiple or all cohorts in an area. Relatively young plant ages on our sites indicated that stand-replacing disturbance processes are still active and that severe insect and drought return intervals may be much shorter than published fire return intervals (32-110 yr) estimated for much of the more arid portions of the Great Basin including Nevada (Wright et al., 1979; Whisenant, 1990). The importance of stand replacement mechanisms other than fire in sagebrush communities may be overlooked as drivers of plant community succession.

Black sagebrush stands were generally older than stands of the other three species, with Wyoming sagebrush the next oldest followed by the two roughly equivalent aged subspecies of *Artemisia arbuscula*. Site variability was only detected for Wyoming sagebrush, indicating that demography trends tend to be similar across relatively broad landscapes. Perryman et al. (2001) found similar age patterns across broad geographic areas for three subspecies of big sagebrush in Wyoming. The site variability detected for Wyoming sagebrush could be due to homestead activities. A postsampling review of homestead records in the Bureau of Land Management database of land patents (Morris, 2012) revealed that a portion of one stand on the SR site was seeded with pasture grass species in 1914, irrigated until 1917, and then abandoned. The current presence of native grass species and the mature stand of sagebrush indicated adequate time to recover from the disturbance. However, the natural pattern of recruitment in that particular stand may have been affected by the soil disturbance (Watts and Wambolt, 1996; Morris et al., 2011).

Regression relationships between black sagebrush recruitment pulses and weather variables at the RP site showed strong relationships with actual precipitation the years before, during, and after recruitment. The amount of precipitation interacts with site quality (e.g., soil depth, water holding capacity) to affect seed production, including total seed number, seed size, and the number of seed heads on a particular sagebrush plant (Beetle, 1960). Large sagebrush seeds typically have an emergence and seedling survival advantage over small seeds (Busso and Perryman, 2005; Busso et al., 2005). This relationship was expected to occur across all species in the assessment since seed production and seedlings easily succumb to droughty conditions; however, results did not entirely support the expected outcome.

April PDO had a strong signal in the simple and/or multiple regressions at six of the sites, while the July PDO had a strong signal at seven sites (minus the black sagebrush RP site where actual precipitation was significant). The July PDO may be an indicator of the strength of the monsoonal weather pattern common to much of south-central and eastern Nevada. We believe that the April and July PDO indices serve as surrogates for actual precipitation occurrence at most of the sites. If so, the alleviation of spring and summer drought is therefore important for understanding sagebrush recruitment patterns in the arid sagebrush communities of the Great Basin.

A Dec-Feb precipitation signal was present for four of the eight sites. Winter precipitation comes as snow and we, like Maier et al. (2001), hypothesize that overwintering snow accumulations can protect sagebrush seedlings from extremely low winter temperatures and wind desiccation. Adverse effects of freezing temperatures on fall and early winter bunchgrass germinants is well documented in the Great Basin and Intermountain West (Arredondo et al., 1998; Boyd and Lemos, 2013). We also believe that the stronger signal of actual precipitation for black sagebrush at the RP site is directly related to ecological site potential including soil water holding capacity. The RP site has higher clay content than the SV site and also has an argillic horizon. These features, especially the argillic horizon, may serve as a moisture reservoir that initially facilitated seedling survival by reducing the time needed for the taproot to reach this horizon before seedling mortality occurs. The argillic and deeper soil layers become the summer and fall maintenance pool for mid- and late-season growth of deep-rooted plants once moisture in the shallow surface horizons is depleted (Ryel et al., 2008).

For Wyoming sagebrush, April and July PDO were predictor variables common to both sites. Since both sites are located near the vertical midline of Nevada, recruitment has likely been influenced by a stronger expression of the summer monsoonal weather pattern that occurs in the middle to eastern half of the state. Low sagebrush sites also had both April and July PDO in common. Soils with an argillic horizon, which low sagebrush prefers (Hironaka et al., 1983; Flerchinger and Cooley, 2000), play a role in available soil moisture during the spring and summer. A strong argillic or clay layer can cause water to be held above the soil profile texture change until that horizon becomes thoroughly wetted (Davies et al., 2007). This allows species with shallow root systems to utilize precipitation from spring events before evaporation occurs (Fetcher and Trlica, 1980). Also, little or no movement of moisture past the argillic horizon accompanied by relatively large moisture levels in the argillic horizon should facilitate root, soil, and moisture contact longer than if the precipitation could rapidly infiltrate past the shallow roots of low sagebrush seedlings. When soil moisture in the profile of thin soils (which are very common on low sagebrush ecological sites) is above average later into the summer months (e.g., years with above-average spring and summer precipitation), there should be a recruitment advantage for shallow-rooted low sagebrush seedlings rather than during the more typical hot and dry summer months when available soil moisture has been depleted (Campbell and Harris, 1977; Booth et al., 2003; Inouye, 2006).

There is no easily identifiable climate-recruitment relationship for Lahontan sagebrush. However, July PDO explained the greatest amount of variation at both locations. The OM site has lithic soils, and the soils at the AF site are shallow to a duripan with an aridic, bordering on xeric soil moisture regime. These harsh edaphic environments undoubtedly limit recruitment of Lahontan sagebrush, and only extreme (infrequent) weather variables can override the edaphic control of recruitment. This condition contributes to low R^2 values for recruitment but also helps explain the relatively large but inconsistent recruitment pulses. On these harsh ecological sites in western Nevada, summer moisture sufficient to recharge even the uppermost region of the soil profile for more than a couple of days is uncommon. The geographic position of these ecological sites excludes them from the typical summer monsoonal pattern. An occasional westward skewing of the pattern increases summer precipitation in that region. A wetter than average summer, indicated by a positive phase July PDO index, would certainly be logical for survival of new Lahontan sagebrush cohorts that emerged during the most recent winter or spring.

All of the PDO variables identified as predictors through regression analysis were positive phase. The positive PDO phase is correlated with above-average precipitation across the entire study area (Gershunov and Barnett, 1998). In the Great Basin the majority of precipitation arrives as snow or very cold rain between late fall and early spring when plants are dormant; however, enhanced summer precipitation has been shown to improve sagebrush recruitment (Gillespie and Loik, 2004). Typically, these summer precipitation events are not single, large events. Rather, their periodicity is more evenly distributed across the growing season (Owens and Norton, 1989), providing a more favorable water-balance for relatively shallow-rooted sagebrush seedlings.

Booth et al. (1990) found that Wyoming big sagebrush seedlings, in a non − water-limiting environment, had a root growth rate that exceeded 1-cm·week^{-1} (maximum = 1.6 cm·week^{-1}) for only the first 8 weeks after emergence. Without sufficient summer precipitation to restore shallow soil moisture for continued growth, sagebrush roots are unlikely to grow long enough to reach the deep soil moisture maintenance pool during the typically dry summer and early fall months. This is critically important when shallow soil water is further depleted by competition from grass species. Perennial bunchgrasses typically have the vast majority of their roots in the surface 15 − 40 cm of the soil (Ganskopp, 1988; Link et al., 1990; Melgoza and Nowak, 1991; Peek et al., 2005) and are well known for extracting most useable soil water by early summer to midsummer (Anderson et al., 1987; Melgoza et al., 1990; Ryel et al., 2010).

Some of the relationships explained by the regression analyses have relatively weak signal power but nevertheless provide insight that helps explain recruitment pulses. Low predictive power can be attributed to the wide ecological amplitude occupied by the sagebrush genera; loss of one or more recruitment cohorts from stand-replacing disturbances such as Aroga moth or age-related mortality; lack of detailed, real-time climate data, especially periodicity of precipitation events; microedaphic variability; the effect of available microhabitat area for recently emerged sagebrush seedlings (Owens and Norton, 1989); and complex or unknown interactions between other biotic and abiotic factors (Noy-Meir, 1973). Weather events that emerge during long-term climate phenomenon such as the positive phase of the PDO index contribute to successful regeneration in sagebrush stands. Likewise, one severe summer drought period may eliminate one or more cohorts of sagebrush seedlings (Owens and Norton, 1989), resulting in little or no recruitment for several years or more, particularly if summer drought return intervals are short.

Demographic variation in other terrestrial plant communities has been attributed to the PDO index (Gedalof et al., 2002; Kaye, 2011). 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 the mid-1990s. The phase shifts in 1925, 1947, and 1977 are a distinct characteristic of the PDO index (Mantua, 1999). In general, the shift from a cool (negative) to a warm (positive) phase of the PDO corresponded with increased sagebrush recruitment.

Implications

In Nevada and the Great Basin, it is imperative that successful sagebrush seeding technologies are discovered and implemented. The climatic relationships identified in this study provide insight into natural recruitment pulses of four sagebrush species. It is important to note that what may seem like recruitment failures due to management activities may in effect only be a product of naturally long periods of time between recruitment pulses. Ecological restoration and postfire rehabilitation methods should be timed correctly with respect to precipitation patterns (positive phase PDO) and/or designed to mimic conditions responsible for natural sagebrush recruitment. This approach, on average, should be more successful and allow valuable and limited resources to be used across multiple restoration challenges rather than the current practice of being used largely on postfire rehabilitation. Our study also advances the current trend in restoration ecology of developing better predictive tools to be used in the restoration of arid and semiarid rangelands (Suding et al., 2004).

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