Demographic Characteristics of Three *Artemisia Tridentata* Subspecies

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Abstract

Previous research suggests that woody plant recruitment may occur in pulses in semi-arid areas. In 1997, approximately 75 stem cross sections were collected from nine stands of each of three subspecies of big sagebrush along elevation and climatic gradients in Wyoming. Annual growth-rings were used to identify year of establishment and demographic characteristics were analyzed from age-class frequencies. Mean stand ages of the three subspecies were different (P=0.002), and subsequent analysis revealed that Wyoming and mountain big sagebrush stand ages (32 $\pm$ 9 and 26 $\pm$ 9 respectively) were significantly older than basin big sagebrush (17 $\pm$ 3) stand ages (LSD, " =0.05). Mean recruitment intervals (years) were shorter for basin (1.6) than for Wyoming (2.3) and mountain (2.2) sagebrush (P=0.01). The number of cohorts did not differ among the subspecies (P=0.11), however, the percent of years with recruitment was significantly higher for basin (59%) compared to Wyoming (37%) and mountain (39%) big sagebrush (P<0.0001). Age-class frequency distributions of each stand and regional stand combination were assessed for dispersion across each associated period of record. Chi-square goodness-of-fit tests were performed for the negative binomial distribution. All stands (with one exception) and all three regional stand combinations fit the negative binomial distribution. Age-class frequency patterns of all subspecies indicate that recruitment is clustered or aggregated across each period of record. Recruitment in big sagebrush stands occurs in pulses throughout Wyoming.

Introduction

All three subspecies of big sagebrush, basin (*Artemisia tridentata* Nutt. ssp. *tridentata*), mountain (*A. tridentata* ssp. *vaseyana* [Rydb.] Beetle), and Wyoming (*A. tridentata* ssp. *wyomingensis* Beetle and Young) are dominant constituents of many rangeland communities, occupying approximately 150,800 square kilometers of rangelands in Wyoming (Beetle and Johnson 1982). Big sagebrush has a wide ecological range and occupies a diversity of habitats (Beetle 1960), playing crucial roles in reducing erosion potential, providing wildlife habitat, and improving rangeland aesthetics (Vale 1974).

Big sagebrush subspecies identification is based on leaf morphology, growth form, and geographic location (Beetle and Johnson 1982). Distribution is related to elevation, temperature, and soil moisture (Cawker 1980). Wyoming sagebrush occurs at low to mid elevations on fine-textured soils. Basin sagebrush is also found at low to mid elevations but on deep, well-developed soils.

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Mountain sagebrush is distributed from mid to high elevations where cooler temperatures, higher precipitation, and developed soils are prevalent (Beetle 1960).

West et al. (1979) concluded that threetip sagebrush (*Artemisia tripartita* Rydb.), and granite pricklygilia (*Leptodactylon pungens* [Torr.] Nutt.) age-class frequency distributions do not usually deviate from the log-normal model, however high recruitment rates were observed in certain years. Pulses of recruitment in desert plant communities were suggested by Went (1955) and demonstrated for creosote bush (*Larrea tridentata* [DC.] Cov.) (Chew and Chew 1965; Barbour 1969). Unusual climatic events and high soil moisture conditions are suggested as major contributing factors (Noy-Meir 1973; Cawker 1980). A pulse is defined as an infrequent recruitment of large numbers of individuals into a population. Cawker (1980) demonstrated evidence of climatic control of big sagebrush survival in British Columbia. If rare or infrequent climatic events control pulses of big sagebrush recruitment, these events should be evident within the population age structure as variations in age class frequency. Demography patterns of big sagebrush in Wyoming have not been assessed. This project was conducted to examine the age structure of nine stands of each of the three subspecies on 27 native sites within three geographic areas of Wyoming.

Specific objectives were to: 1) determine plant and stand ages; 2) compare stand ages, periods of record, number of cohorts, percent of years with recruitment, and recruitment intervals between subspecies; and 3) assess the dispersion of age-class frequencies through time.

Materials and Methods

Big sagebrush stands having a variety of cohorts, similar soil characteristics and topography, and minimal herbivory disturbance were selected for this study. Sites were selected to minimize microsite effects that increase or decrease supplemental moisture conditions, thereby minimizing potential variations in recruitment and survival rates between sites (Roughton 1972; Bonham et al. 1991).

Stem sections for *wyomingensis* were collected from three stands in northeast Wyoming near Rochelle; three stands in the South Fork of the Powder River watershed, northwest of Casper in central Wyoming; and three stands in southwest Wyoming near Pinedale. Stem sections for *tridentata* were collected from three stands near Pinedale; three stands near Worland, on the west slope of the Bighorn Mountains; and three stands near Farson, in southwest Wyoming. Stem sections for *vaseyana* were collected from three stands near Pinedale; three stands near Buffalo, on the east slope of the Bighorn Mountains; and three stands west of Laramie, near Elk Mountain in south central Wyoming. The three stands in each regional grouping were located within a 15 mile radius. All stand locations were permanently recorded with a Global Positioning System, and latitude/longitude coordinates and elevations were reported by Perryman and Olson (2000).

A stratified, random sampling method was used to collect stem cross-sections from each stand. A permanent 100 m baseline transect was located within each stand, and 10, 100 m 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 big sagebrush plant was sampled. If the closest individual was not suitable for accurate age determination (e.g., damaged stem), another random point was selected until a suitable individual was found.

Stem cross-sections were obtained by sawing the plant below ground level (Ferguson 1964) to ensure that the pith and first annual growth ring were included. The stem was then cut approximately 10 cm from the bottom, providing a 10 cm long stem section. Sampling was conducted during the summer of 1997. Between 75 and 80 stem sections were collected from each stand (Cawker 1980).

In the laboratory, the bottom portion of each stem section was sanded sequentially with 60, 80, 320, and 400 grit sanding belts. Annual growth-rings were examined using a 10 power stereo microscope, and enumerated once by two different technicians for a total of two observations per sample.

Annual growth-rings are formed when the secondary xylem forms concentric rings around the stem during the growing season. Rings are easily distinguishable from one another by a distinct cork layer 8-18 cells wide (Ferguson 1964). This layer is produced throughout the growing season between the old and new xylem.

Inter-annual or false rings have not been encountered in big sagebrush at northern latitudes and higher elevations (Diettert 1938, Moss 1940, Ferguson 1964, Perryman and Olson 2000). Global positions and elevation of sites in Wyoming fulfill both of these criteria. Locally absent rings do occur, however complete absence of rings are almost never encountered due to the unique nature of annual growth-ring formation in big sagebrush (Ferguson 1964, Perryman and Olson 2000).

Many older stems are “lobed” or “rosette” in form and lack radial symmetry. Often the decumbent and decadent form of older stems leads to open pith exposure and loss. Accurate age assessments are not possible when the pith is absent. Our sampling was biased for single-stemmed plants with intact piths over individuals without radial symmetry. As a result, some older plants with decadent stems were excluded.

Mean recruitment intervals, period of record, number of cohorts, and percent of years with recruitment were calculated for each subspecies. Age-class frequency distributions were constructed for each subspecies at 2 geographic scales, stand and regional stand combination. Age-class frequency dispersion through time was assessed by chi-square goodness-of-fit tests for both Poisson and negative binomial distributions (Ludwig and Reynolds 1988; Zar 1999).

Results and Discussion

Individual plants and stands were generally younger than those found in previous big sagebrush dendrochronologic studies (Ferguson 1964, Roughton 1972, Cawker 1980). Prior research indicated that individual big sagebrush plant age often exceeds 100 years (Blaisdell 1953, Ferguson 1964) in the southwestern U.S. The oldest plant (81 years) in this study was a mountain sagebrush plant located in the Bighorn Mountains. The oldest Wyoming sagebrush plant (75 years) was from the Powder River Basin, and the oldest basin sagebrush plant (55 years) was found near Pinedale, WY. Young seedlings, 5-10 years old, were common in all stands.

Analysis of variance indicated that mean stand ages of the three subspecies were different (P= 0.002), and subsequent analysis revealed that Wyoming and mountain sagebrush stand ages (32, $\pm$ 9 and 26, $\pm$ 9 years respectively) were older than basin sagebrush (17, $\pm$ 3) stand age (LSD, α=0.05). Mean and median ages for stands and geographic stand combinations by subspecies are listed in Table 1. Analysis of variance indicated no difference in stand ages between geographic region (P=0.60).

Table 1. Mean and median stand and regional stand combination ages (years) by subspecies in Wyoming, 1997.

Subspecies, Stand, and Regional Combination	Mean	Median	n
wyomingensis			
R1	28	25	78
R2	23	19	73
R3	26	28	73
Northeast WY	26	25	224
TT1	32	33	61
TT2	30	29	58
TT3	21	16	59
Central WY	27	29	178
MW1	45	46	69
MW2	50	50	65
MW3	39	39	67
Southwest WY	45	46	201
vaseyana			
EM1	19	19	67
EM2	21	17	69
EM3	26	18	69
Southcentral WY	22	18	205
ES1	23	19	67
ES2	15	16	81
ES3	17	17	76
Central WY	18	17	224
P1	44	47	60
P2	34	35	57
P3	31	25	67
Southwest WY	36	35	184
tridentata			
WS1	22	21	76
WS2	22	21	70
WS3	14	13	78
Central WY	19	21	224
BS1	20	20	70
BS2	15	14	73
BS3	14	12	68
Southwest WY[1]	17	14	211
BP1	14	13	74
BP2	17	17	76
BP3	16	16	72
Southwest WY[2]	16	16	222

[1]West slope of the Green River Basin [2]East slope of the Green River Basin

Analysis of variance results for recruitment intervals, period of record, number of cohorts, and percent of years with recruitment are in Table 2. Recruitment intervals (by stand) ranged from 1.9 to 2.7 years for Wyoming sagebrush; 1.3 to 2.7 for basin sagebrush; and 1.2 to 2.9 for mountain sagebrush. Mean recruitment intervals were shorter for basin sagebrush (1.6) than for Wyoming (2.3) and mountain (2.2) sagebrush (P= 0.01). Years with high age-class frequencies occurred at irregular intervals. This supports the hypotheses by Went (1955) and West et al. (1979) that successful recruitment in arid and semi-arid plant communities occurs in pulses, often with many years of no seedling survival between successful years. Shorter intervals reflect more frequent, favorable recruitment conditions and higher rates of seedling survival. Less favorable climatic conditions may lengthen intervals in regions where Wyoming and mountain sagebrush plants occur (West 1978, Cawker 1980).

The number of cohorts did not differ among the subspecies (P= 0.11), however, the percent of successful recruitment years was significantly higher for basin sagebrush (59%) than for the Wyoming (37%) and mountain (39%) subspecies (P< 0.0001). A shorter mean period of record for basin sagebrush may explain the higher recruitment rate and shorter recruitment intervals. However, big sagebrush recruitment is episodic, and our data suggest that for Wyoming big sagebrush, statewide recruitment occurred in only 33 of the past 75 years.

Table 2. Mean recruitment intervals (years), mean number of cohorts in the period of record, mean percent of recruitment years in the period of record, and mean period of record (years) by subspecies sampled across 27 sites in Wyoming, 1997.

Subspecies	Interval (yr)[1]	# of Cohorts	% Recruitment Years	Period of Record
wyomingensis	2.3^{a} (± 0.7)	23^{a} (± 1.9)	37^{a} (± 5)	62 (± 6)
vaseyana	2.2^{a} (± 0.7)	21^{a} (± 4.1)	39^{a} (± 6)	54 (± 14)
tridentata	1.6^{b} (± 0.6)	20^{a} (± 2.4)	59^{b} (± 9)	34 (± 8)

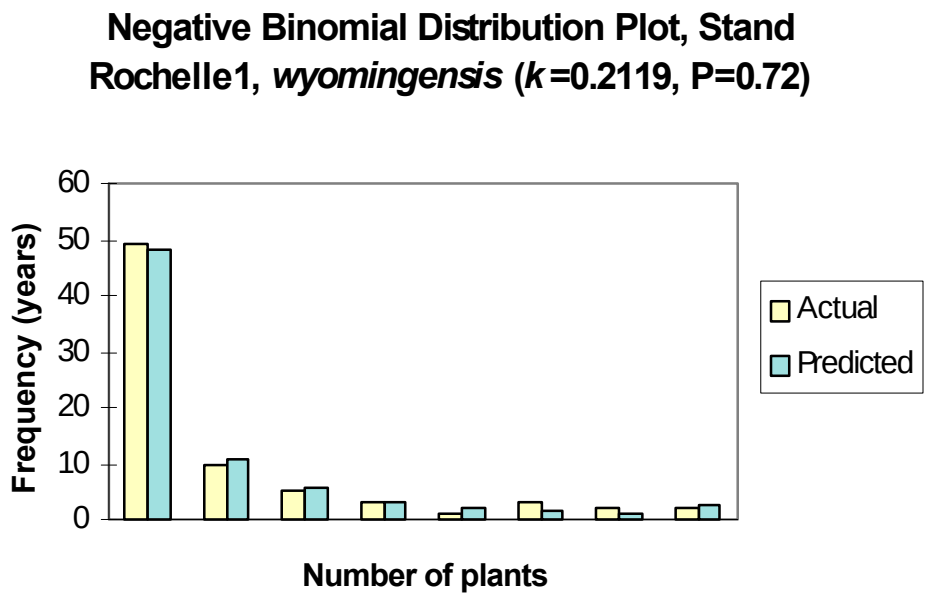
[1] Means with the same superscript within a column are not significantly different (P>0.05, LSD).

Age-class frequency distributions of each stand and regional stand combination were assessed for dispersion across each associated period of record. Chi-square goodness-of-fit tests were performed for both the Poisson and negative binomial distributions (Table 3). No stands or regional stand combinations fit the Poisson distribution and all variances were greater than the mean, indicating that recruitment is not random, but clustered, aggregated, or contagious (Zar 1999) across a period of record. All stands (with the exception of one mountain sagebrush stand) and all three regional stand combinations fit the negative binomial distribution. Means were different for each stand and stand combination so k-exponent values were different for each goodness-of-fit test (Table 3).

Cohort or age-class negative binomial distribution patterns were characterized by a relatively large number of years with no recruitment, a moderate number of years with minimal recruitment, and relatively few years with relatively high recruitment. Graphs of actual frequency probabilities for a representative stand and regional stand combination are displayed in Figure 1.

Fig. 1. Negative binomial distribution plots from Chi-square goodness-of-fit tests of (a) a representative stand and (b) a regional combination of stands for Wyoming sagebrush, sampled in northeast Wyoming, 1997.

(a)



(b)

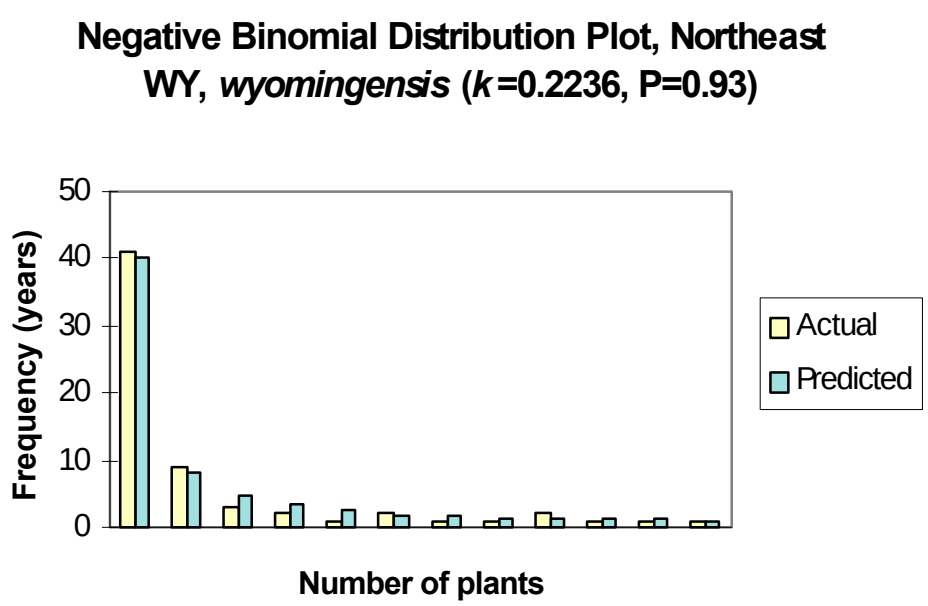


Table 3. Results of Chi-square goodness-of-fit tests for the negative binomial (p-value and k-exponent value) distribution of individual stands and regional stand combinations, across Wyoming, 1997. (Poisson distribution tests were all significant at $P \leq 0.0001$).

Stand, and Regional Combination	Negative Binomial	*k*
wyomingensis		
Rochelle1	0.22	0.2387
Rochelle2	0.83	0.2119
Rochelle3	0.64	0.2145
Northeast WY (Rochelle 1,2,3 combined)	0.50	0.2236
TT Ranch1	0.19	0.3612
TT Ranch2	0.23	0.5818
TT Ranch3	0.44	0.3962
Southwest WY (TT Ranch 1,2,3 combined)	0.35	0.5377
Midwest1	0.75	0.2499
Midwest2	0.32	0.3043
Midwest3	0.56	0.3218
Central WY (Midwest 1,2,3 combined)	0.71	0.3667
vaseyana		
Elk Mountain1	0.56	0.4662
Elk Mountain2	0.99	0.3052
Elk Mountain3	0.32	0.2348
Southcentral WY (Elk Mtn. 1,2,3 combined)	0.67	0.2674
East Slope1	0.23	0.3029
East Slope2	0.59	0.1538
East Slope3	0.84	0.2509
Central WY (East Slope 1,2,3 combined)	0.45	0.1659
Pinedale1	0.91	0.2337
Pinedale2	0.81	0.3322
Pinedale3	0.009*	0.3480
Southwest WY (Pinedale 1,2,3 combined)	0.34	0.3698
tridentata		
West Slope1	0.31	0.4497
West Slope2	0.51	0.4889
West Slope3	0.54	0.4069
Central WY (West Slope 1,2,3 combined)	0.11	0.4111
Big Sandy1	0.14	1.2299
Big Sandy2	0.76	0.3408
Big Sandy3	0.68	0.6599
Southwest WY[1] (Big Sandy 1,2,3 combined)	0.318	0.683
Big Piney1	0.40	0.6382
Big Piney2	0.69	0.4016
Big Piney3	0.79	0.2247
Southwest WY[2] (Big Piney 1,2,3 combined)	0.87	0.2403

[1]West slope of the Green River Basin [2]East slope of the Green River Basin
*Only stand or stand combination that did not fit the negative binomial distribution.

Conclusion

These results suggest that big sagebrush plants that dominate much of the current vertical structure of plant communities in Wyoming are relatively young. However, mean stand ages of Wyoming big sagebrush in northeast and central Wyoming are approximately 3 to 4 times older than the mean fire-free interval (8 years) for the area (Perryman 1996). Fire suppression activities are often associated with woody plant invasion of northern mixed-grasslands (Kucera 1981; Fisher et al. 1987; Steinaur and Bragg 1987).

Irregular pulses of recruitment are characteristic of big sagebrush stands in Wyoming. These results support hypotheses by Went (1955), West et al. (1979), and Cawker (1980), that recruitment in semi-arid regions occur only in years with favorable climate. Age-class frequency of big sagebrush stands follow the negative binomial distribution. Characteristically, there are a large number of years of no recruitment, an intermediate number of years with some recruitment, and a few years of high recruitment. Recruitment intervals are longer for Wyoming and mountain big sagebrush than for basin big sagebrush. We believe these results reflect general trends of demography in other big sagebrush communities in Wyoming. The large sample size (approximately 2200 individual plants) and regional consistency of results support our conclusion.

Future research must address mortality and survivorship curves of big sagebrush to fully understand the demography of this species. However, this study describes age frequency distributions and pulse recruitment phenomena of big sagebrush in Wyoming.

References

Barbour, M.G. 1969. Age and space distribution of the desert shrub *Larrea divaricata*. Ecology 50:679-685.

Beetle, A. A. 1960. A study of sagebrush, the section *Tridentatae* of *Artemisia*. Wyoming Agr. Exp. Sta. Bull. No. 368, Laramie.

Beetle, A. A. and K. L. Johnson. 1982. Sagebrush in Wyoming. University of Wyoming, Wyo. Agr. Exp. Sta. Bull. No. 779, Laramie.

Blaisdell, J.P. 1953. Ecological effects of planned burning of sagebrush-grass range on the Upper Snake River Plains. U.S. Dept. of Agr. Tech. Rep. No. 1075. U.S. Government Printing Office, Washington, D.C.

Bonham, C.D., T.R. Cottrell, and J.F. Mitchell. 1991. Inferences for life history strategies of *Artemisia tridentata* subspecies. J. of Veg. Sci. 2:339-344.

Cawker, K.B. 1980. Evidence of climatic control from population age structure of *Artemisia tridentata* Nutt. in southern British Columbia. J. of Biogeogr. 7:237-248.

Chew, R.M. and A.E. Chew. 1965. The primary productivity of a desert shrub (*Larrea tridentata*) community. Ecol. Monogr. 35:355-375.

Diettert, R.A. 1938. The morphology of *Artemisia tridentata* Nutt. Lloydata 1:3-74.

Ferguson, C.W. 1964. Annual rings in big sagebrush. Papers of the Laboratory of Tree-Ring Research No. 1. The University of Arizona Press, Tucson.

Fisher, R.F., J.J. Jenkins, and W.F. Fisher. 1987. Fire and the prairie-forest mosaic of Devil's Tower National Monument. Am. Mid. Nat.117:250-257.

Kucera, C.L. 1981. Grasslands and fire. *In*: Fire Regimes and Ecosystem Properties. USDA For. Serv. Gen. Tech. Rep. WO-26, 594p.

Ludwig, J.A. and J.F. Reynolds. 1988. Statistical Ecology: A Primer on Methods and Computing. John Wiley & Sons, New York.

Moss, E.H. 1940. Interxylary cork in *Artemisia* with reference to its taxonomic significance. Am. J. Bot. 27:762-768.

Noy-Meir, I. 1973. Desert ecosystems: environment and producers. Annual Review of Ecology and Systematics. 4:25-51.

Perryman, B.L. 1996. Fire history of the Rochelle Hills area of Thunder Basin National Grasslands. Ph.D. Dissertation, Univ. of Wyoming, Laramie.

Perryman, B.L. and R.A. Olson. 2000. Age-stem diameter relationships of big sagebrush and their management implications. J. Range. Manage. 53:342-346.

Roughton, R.D. 1972. Shrub age structures on a mule deer winter range in Colorado. Ecology. 53:615-625.

Steinauer, E.M. and T.B. Bragg. 1987. Ponderosa pine (*Pinus ponderosa*) invasion of Nebraska Sandhills prairie. Am. Mid. Nat. 118:358-365

Vale, T.R. 1974. Sagebrush conversion projects: An element of contemporary environmental change in the western United States. Biol. Conserv. 6:274-284.

Went, R.W. 1955. The ecology of desert plants. Sci. Amer. 192:68-75.

West, N.E. 1978. Basic synecological relationships of sagebrush dominated lands in the Great Basin and Colorado plateau. pp. 33-41. *In* The sagebrush ecosystem, A symposium, Logan, UT, College of Natural Resources, Utah State Univ., Logan.

West, N.E., K.H. Rea, and R.O. Harniss. 1979. Plant demographic studies in sagebrush-grass communities of southeastern Idaho. Ecology 60:376-388.

Zar, J.H. 1999. Biostatistical Analysis, 4th Ed. Prentice Hall, Upper Saddle River, NJ