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Demographic characteristics of 3 *Artemisia tridentata* Nutt. subspecies

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Abstract

Previous research suggested that woody plant recruitment may occur in pulses in semi-arid areas. The overall objective of this study was to determine if this pulse phenomena was recorded in the demographic structures of big sagebrush (*Artemisia tridentata* Nutt.) stands in Wyoming. In 1997, approximately 75 stem cross sections were collected from 9 stands of each of 3 subspecies of big sagebrush in Wyoming along elevation and climatic gradients. Annual growth-rings were used to identify year of establishment and demographic characteristics were analyzed from age-class frequencies. Mean stand ages of the 3 subspecies were different (P = 0.002), and analyses revealed that Wyoming (*A. tridentata* ssp. *wyomingensis*) and mountain big sagebrush (*A. tridentata* ssp. *vaseyana*) stand ages (32 ± 9 and 26 ± 9 years, respectively) were significantly older than basin big sagebrush (*A. tridentata* ssp. *tridentata*) (17 ± 3) stands (P < 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), but the percent of years with recruitment was significantly higher for basin (59%) compared to Wyoming (37%) and mountain (39%) subspecies (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 3 regional stand combinations fit the negative binomial distribution. Age-class frequency patterns indicate that recruitment is clustered or aggregated across each period of record. Recruitment in big sagebrush stands occurs in pulses throughout Wyoming.

Key Words: demography, big sagebrush, recruitment intervals

Resumen

Investigación previa sugiere que en áreas aridas y semiáridos el establecimiento poblaciones de plantas leñosas puede ocurrir en pulsos. El objetivo general de este estudio fue determinar si este fenómeno de pulsos se registro en la estructura demográfica de poblaciones de "Big sagebrush" (*Artemisa tridentata* Nutt.) situadas en Wyoming. En 1997 se colectaron aproximadamente 75 secciones transversales de tallos de 9 poblaciones de cada una de las 3 subespecies de "Big sagebrush" presentes en Wyoming, la colecta se realizó a lo largo de gradientes climáticos y de elevación. Se utilizaron los anillos de crecimiento anual para identificar el año de establecimiento y las características demográficas se analizaron mediante frecuencias de edad-clase. La edad media de las 3 subespecies fue diferente (P = 0.002) y los análisis revelaron que las edades de las poblaciones de las subespecies "Wyoming" (*A. tridentata* ssp. *wyomingenesis*) y "Mountain big sagebrush" (*A. tridentata* ssp. *vaseyana*) (32 ± 9 y 26 ± 9 años, respectivamente) fueron significativamente mayores que la edad de las poblaciones de la subespecie "Basin big sagebrush" (*A. tridentata* ssp. *tridentata*) (17 ± 3) (P < 0.05). Los intervalos de establecimiento (años) fueron mas cortos para la subespecie "Basin big sagebrush" (1.6) que los de las subespecies "Wyoming" (2.3) y "Mountain big sagebrush" (2.2) (P = 0.01). El numero de generaciones no difirió entre subespecies (P = 0.11), pero el porcentaje de años con establecimiento de plantas fue significativamente mayor para la subespecie "Basin big sagebrush" (59%) que el de las subespecies "Wyoming"(37% y "Mountain big sagebrush" (39%) (P = 0.0001). Las distribuciones de frecuencia de edad-clase de cada población y la combinación regional de poblaciones se evaluó para ver la dispersión a través de cada periodo asociado con el registro. Se efectuaron pruebas de bondad de Chi-cuadrada para la distribución binomial negativa. Todas las poblaciones (excepto una) y todas las 3 combinaciones regionales de poblaciones tuvieron un distribución binomial negativa. Los patrones de frecuencia edad-clase indican que el establecimiento es aglomerado o agregado a través de cada periodo de registro. El establecimiento de poblaciones de "Big sagebrush" ocume en pulsos a través de Wyoming.

All 3 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) characterize many rangeland communities, occupying about 150,800 km^2 of rangelands in Wyoming (Beetle and Johnson 1982). Big sagebrush has a wide ecological amplitude and occupies a diversity of habitats (Beetle 1960), playing crucial roles in reducing erosion, providing wildlife habitat, and improving rangeland aesthetics (Vale 1974).

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 at low to mid elevations but on deep, well-developed soils; and mountain

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

Pulses of recruitment in desert plant communities was suggested by Went (1955) and demonstrated for creosote bush (*Larrea tridentata* [DC.] Cov.) (Chew and Chew 1965, Barbour 1969), for threetip sagebrush (*Artemisia tripartita* Rydb.) and granite pricklygilia (*Leptodactylon pungens* [Torr.] Nutt.) (West et al. 1979). Unusual climatic events and high soil moisture conditions are suggested as major contributing factors (Noy-Meir 1973, Cawker 1980). A pulse is an infrequent recruitment of many 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 stand age structures as variations in age class frequency. Demography patterns of big sagebrush in Wyoming have not been assessed. Concerns about wildlife species obligate to big sagebrush and declining habitat quantity/quality require a comprehensive understanding of big sagebrush ecology.

This project was conducted to examine the age structure of 9 stands of each of the 3 subspecies on 27 native sites within 3 geographic areas of Wyoming. Specific objectives were to: 1) determine individual 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

Mature big sagebrush stands having 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 3 stands in northeast Wyoming near Rochelle; 3 stands in the South Fork of the Powder River watershed, northwest of Casper in central Wyoming; and 3 stands in southwest Wyoming near Pinedale. Stem sections for *tridentata* were collected from 3 stands near Pinedale; 3 stands near Worland, on the west slope of the Bighorn Mountains; and 3 stands near Farson, in southwest Wyoming. Stem sections for *vaseyana* were collected from 3 stands near Pinedale; 3 stands near Buffalo, on the east slope of the Bighorn Mountains; and 3 stands west of Laramie, near Elk Mountain in south central Wyoming. The 3 stands in each regional grouping were located within a 15 mile radius. All stand coordinates were determined with a Global Positioning System, and are published in 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 ten, 100-m perpendicular transects were established at randomly selected points along the baseline transect. Along each perpendicular transect, 8 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 above the first cut, yielding 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 2 different technicians for a total of 2 observations per sample.

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

Subspecies, Stand, and Regional Combination	Mean	Median	n
wyomingensis			
Stand Rochelle1	28	25	78
Stand Rochelle2	23	19	73
Stand Rochelle3	26	28	73
Northeast WY (Rochell1,2,3 combined)	26	25	224
Stand TT Ranch1	32	33	61
Stand TT Ranch2	30	29	58
Stand TT Ranch3	21	16	59
Southwest WY (TTRanch1,2,3 combined)	27	29	178
Stand Midwest1	45	46	69
Stand Midwest2	50	50	65
Stand Midwest3	39	39	67
Central WY (Midwest1,2,3 combined)	45	46	201
vaseyana			
Stand Elk Mountain1	19	19	67
Stand Elk Mountain2	21	17	69
Stand Elk Mountain3	26	18	69
Southcentral WY (Elk Mountain1,2,3 combined)	22	18	205
Stand East Slope1	23	19	67
Stand East Slope2	15	16	81
Stand East Slope3	17	17	76
Central WY (East Slope1,2,3, combined)	18	17	224
Stand Pinedale1	44	47	60
Stand Pinedale2	34	35	57
Stand Pinedale3	31	25	67
Southwest WY (Pinedale1,2,3 combined)	36	35	184
tridentata			
Stand West Slope1	22	21	76
Stand West Slope2	22	21	70
Stand West Slope3	14	13	78
Central WY (West Slope1,2,3 combined)	19	21	224
Stand Big Sandy1	20	20	70
Stand Big Sandy2	15	14	73
Stand Big Sandy3	14	12	68
Southwest WY[1] (Big Sandy1,2,3 combined)	17	14	211
Stand Big Piney1	14	13	74
Stand Big Piney2	17	17	76
Stand Big Piney3	16	16	72
Southwest WY[2] (Big Piney1,2,3 combined)	16	16	222

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

Annual growth-rings are formed when the secondary xylem forms concentric rings around the stem during the growing season. Rings are easily distinguished 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). Location and elevation of sites in Wyoming fulfill both of these criteria. Locally absent rings do occur, however complete absence of rings is 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 deterioration. 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, periods of record, number of cohorts, and percent of years with recruitment were determined for each subspecies on a statewide scale and assessed with one-way analysis of variance. Multiple comparisons of means were performed using the least significant difference (LSD) test (Saville 1990). 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 (random) and negative binomial (clustered/aggregated) distributions (Ludwig and Reynolds 1988, Zar 1999). All analyses were determined significant at $P < 0.05$.

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 big sagebrush plant age often exceeds 100 years (Blaisdell 1953, Ferguson 1964) in the southwestern U.S. The oldest individual (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, Wyo. Young seedlings, 5–10 years old, were common in all stands. Sampling bias for plants with intact piths may have potentially lowered mean stand ages, however, both younger and older plants were excluded when they lacked intact piths.

Analysis of variance indicated that mean stand ages of the 3 subspecies were differ-

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.

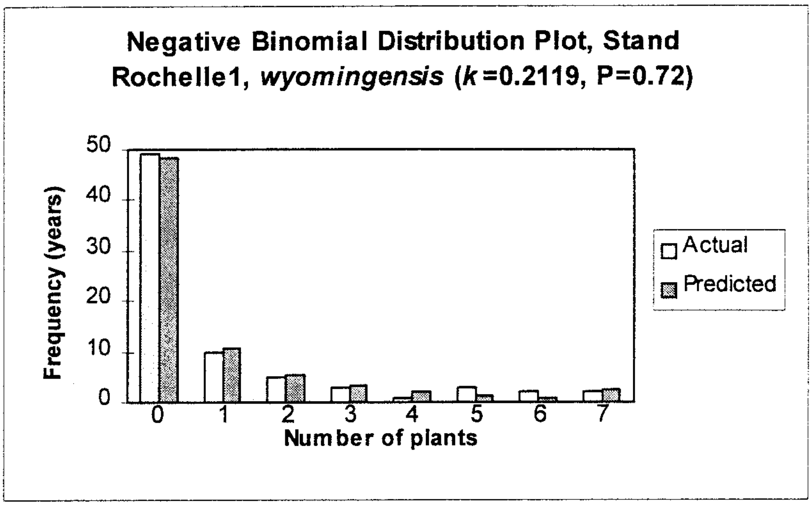
Subspecies	Interval[1]	Cohorts	Recruitment Years	Period of Record
	(YR)	(No.)	(%)	(YR)
wyomingensis	2.3[a] (± 0.7)	23[a] (± 1.9)	37[a] (± 5)	62 (± 6)
vaseyana	2.2[a] (± 0.7)	21[a] (± 4.1)	39[a] (± 6)	54 (± 14)
tridentata	1.6[b] (± 0.6)	20[a] (± 2.4)	59[b] (± 9)	34 (± 8)

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

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 $P < 0.0001$).

Stand, and Regional Combination	P-value	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)	0.31	0.6838
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.



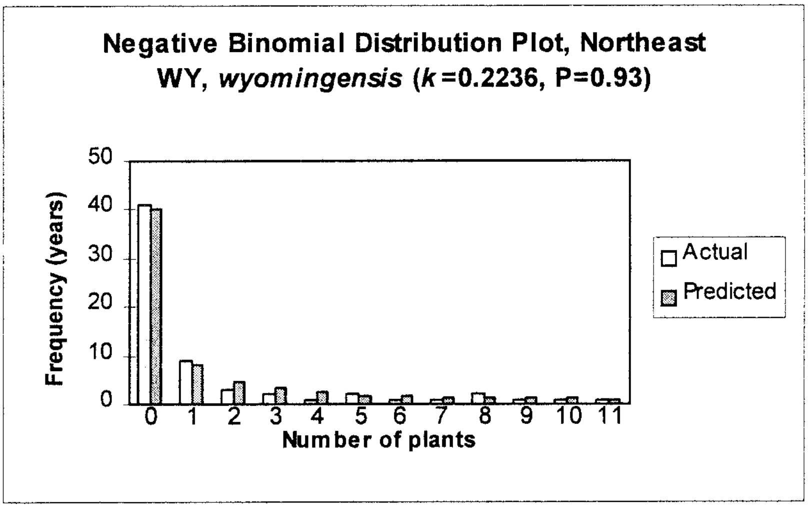


Fig. 1. Negative binomial distribution plots from Chi-square goodness-of-fit tests of (a) a representative stand and (b) a regional combination of stands for Wyoming sagebrush, sampled in northeast Wyoming, 1997.

ent, and the LSD test revealed that Wyoming and mountain sagebrush stands (32, ± 9 and 26, ± 9 years respectively) were older than basin sagebrush (17, ± 3) stands. Mean and median ages for stands and geographic stand combinations by subspecies are listed in Table 1. No difference in stand ages occurred among geographic region (P = 0.60).

Mean recruitment intervals, period of record, number of cohorts, and percent of years with recruitment are in Table 2. Stand recruitment intervals ranged from 1.9 to 2.7 years for Wyoming sagebrush; 1.3 to 2.7 years for basin sagebrush; and 1.2 to 2.9 years for mountain sagebrush. Mean recruitment intervals were shorter for basin sagebrush (1.6 years) than for Wyoming (2.3 years) and mountain (2.2 years) sagebrush. 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 subspecies, but the percent of successful recruitment years was significantly higher for basin sagebrush (59%) than for the Wyoming (37%) and mountain (39%) subspecies). The 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 sagebrush, statewide recruitment occurred in only 33 of the past 75 years.

Age-class frequency distributions of each stand and regional stand combination were assessed for dispersion across each associated period of record. No stands or regional stand combinations fit the Poisson distribution (P < 0.0001) and all variances were greater than the mean, indicating recruitment is not random, but clustered, aggregated, or contagious (Zar 1999) across a period of record. With the exception of 1 mountain sagebrush stand, all stands and all three regional stand combinations fit the negative binomial distribution. Means were different for each stand and stand combination so *k*-exponent values also differed 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 some 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 Fig. 1.

Conclusion

We suggest that big sagebrush plants dominating much of the current vertical structure of plant communities in Wyoming are relatively young. However, mean stand ages of Wyoming 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 and Laycock 2000). 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 occurs in pulses consistent with favorable climate. Other factors such as fire, insect outbreaks, herbivory, and understory composition may also affect demography patterns. However, without favorable weather, recruitment pulses may not occur.

Age-class frequency of big sagebrush stands approximate 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 sagebrush than for basin sagebrush. We believe these results reflect general trends of demography in other big sagebrush communities in Wyoming. Our large sample size (approximately 2200 individual plants) and regional consistency of results support our conclusion.

This study describes age-class frequency distributions and pulse recruitment phenomena of big sagebrush in Wyoming. However, future research must address mortality, survivorship curves, and the identification of climatic controls responsible for recruitment pulses of big sagebrush to fully understand the demography of this species.

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