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PLANT AGE/SIZE DISTRIBUTIONS IN BLACK SAGEBRUSH (ARTEMISIA NOVA): EFFECTS ON COMMUNITY STRUCTURE

James A. Young¹ and Debra E. Palmquist¹

ABSTRACT.—The demography of black sagebrush (Artemisia nova Nelson) was investigated in the Buckskin Mountains of western Nevada to determine patterns of stand renewal in sagebrush communities currently free from wildfires. Biomass sampling was conducted to develop growth classes that reflected apparent age of the shrubs. The density of black sagebrush plants was twice that of basin big sagebrush (A. tridentata ssp. tridentata Nutt.) in adjacent communities on contrasting soils (2.2 versus 1.1 plants per m²). Black sagebrush accumulated only 75% as much woody biomass as big sagebrush.

Regression equations were developed and tested for predicting total woody biomass, current annual growth (CAG), and leaf weight of black sagebrush plants. Apparent age classes were developed both for the black sagebrush plants and the sub-canopy mounds on which they grew. Discriminant analysis was used to test this classification system. Plant succession, apparently controlled by nitrate content of the surface soil, appeared to eliminate the successful establishment of black sagebrush seedlings on the mounds. After the shrubs die, the mounds eventually deflate. We propose that mounds reform around shrub seedlings; but because seedling establishment is so rare in these communities, this could not be verified.

Key words: biomass, shrub succession, desert soil formation, soil nitrate, black sagebrush, Artemisia nova.

Black sagebrush (Artemisia nova Nelson) is one of the dwarf sagebrush species which collectively constitute about half the sagebrush vegetation in Nevada (Beetle 1960). Black sagebrush plays a dominant role in a number of plant communities in the Great Basin (Zamora and Tueller 1973). Rarely does black sagebrush share dominance with another species of Artemisia. In the section Tridensate of the genus Artemisia, black sagebrush is perhaps the species most adapted to arid environments. Black sagebrush is closely associated with shadscale [Atriplex confertifolia (Torr. & Frem.) Wats.] dominated landscapes (Blaisdell and Holmgren 1984). The browse of black sagebrush is highly preferred by domestic sheep (Ovis aries), pronghorn (Antilocapra americana), and Sage Grouse (Centrocercus urophasianus). From the 1890s until the late 1950s, black sagebrush plant communities in the Carson Desert of Nevada were a vital part of winter range for the domestic range sheep industry. Years of excessive browsing by sheep actually shaped the outline of black sagebrush shrub canopies; Zamora and Tueller (1973) reported they had difficulty in finding relic communities in high range condition.

Vegetation of the Buckskin Mountains of west central Nevada is characterized by black sagebrush/desert needlegrass (Stipa speciosa Trin. & Rupr.) plant communities. The Buckskin Mountains are located 100 km southeast of Reno, Nevada, in the rain shadow of both the Sierra Nevada and Pinenut Mountains. This is a portion of the Carson Desert in which Billings (1945) suggested that Atriplex-dominated salt desert shrub vegetation occurred because of atmospheric drought rather than occurrence of soluble salts in the soil. If we compare the black sagebrush communities of the Buckskin Mountains with those described in the regional study conducted by Zamora and Tueller (1973), we find that the highest-elevation, north-facing slope communities of the Buckskin Mountains correspond to the most arid communities previously described. From this we assume the black sagebrush communities in this study represent an arid extension of this type.

Only recently have occasional wildfires of any extent occurred in black sagebrush communities in western Nevada. The fires that have occurred have been associated with the recent spread of the alien annual cheatgrass (Bromus tectorum L.) into these arid environments (Young and Tipton 1990). Apparently for much

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of the twentieth century these communities have not been subject to wildfires because of lack of herbaceous vegetation to carry the fire. Because of the lack of trees to produce fire scars, it is difficult to determine whether these sites were subject to periodic burning under pristine conditions. This is in sharp contrast to basin big sagebrush communities where periodic catastrophic stand renewal by burning from wildfires has been common. The lack of catastrophic stand renewal in black sagebrush communities should be reflected in the age/size class structure of the communities.

Our purpose was to determine the age/size distribution of black sagebrush plants to determine community structure.

MATERIALS AND METHODS

Studies were conducted from 1984 through 1988 in the Buckskin Mountains located about 100 km southeast of Reno, Nevada. The geologic features of this mountain range have been described in detail by Hudson and Oriel (1979). Vegetation and soils of the range have been mapped and related to the geologic map of the area (Lugaski and Young 1988). The plant communities used in this study were located on the Guild Mine member of the Mickey Pass tuff. This geologic unit consists of crystal-rich, moderately to poorly welded ash flow tuff (Proffett and Proffett 1976). It has been proposed that the soils (a) developed in place, (b) developed from subaerially deposited material from long-distance transportation, or (c) developed from a combination of residual and subaerially deposited material (unpublished research, ARS-USDA). The bulk of the profile is an argillic horizon, about 50 cm thick, which consists of 50% or more clay-textured material. It is proposed that this clay horizon is a relic of a soil that developed on the site and whose original surface horizon has been removed by erosion. The important point is that the clay horizon, which is intermittently exposed on the soil surface, developed under different environmental conditions from the current surface horizon. The current surface soil consists of a relatively recently deposited layer, apparently from subaerial deposition, that is largely confined to mini-mounds beneath the canopies of the black sagebrush plants. The soil is classified as a fine, iridic, montmorillonitic, Typic Paleargid.

Spatial structure of the black sagebrush communities was determined by sampling five stands located along the western flank of the Buckskin Mountains. The five stands, located on the same outcropping of Mickey Pass tuff, were separated by small canyons where the westerly tilted ash flows were broken by faulting. All sites were west facing and located in a band along the mountainside at 1720–1780-m elevation.

A starting point was located on aerial photographs in each stand, and 10 plots, each 10 m² in area, were located randomly along line transects parallel to the slope. A total of 50 plots were established (5 stands x 10 plots per stand). In each plot the following were determined: (a) shrub density by species, (b) crown cover of shrubs (ocular estimate), (c) shrub height, (d) area of mound and interspaces, and (e) herbaceous cover (ocular estimate). Mound cover refers to the slightly raised areas beneath shrub canopies where subaerially deposited soil and saltation deposits accumulate.

At each plot location the herbaceous vegetation frequency was sampled with 100 step points arranged in 4 lines of 25 points each following the procedures of Evans and Love (1957). The herbaceous vegetation was resampled annually.

Using the same starting point, but by placing the transects up and down the slope, 25 black sagebrush mounds were located in each stand. The shrubs rooted on each mound were measured for (a) height, (b) maximum and minimum crown diameter, (c) stem number (as black sagebrush ages the cambium splits, forming multiple-stemmed plants), and (d) stem diameter at the soil surface (diameter of the group of split stems). The aerial portion of the plant was subdivided by clipping into the following categories: (a) coarse stems, 2.5 cm or larger in diameter; (b) fine stems, 0.25 to 2.4 cm in diameter; (c) current annual growth; and (d) leaves. The material was dried at 80 degrees C for 24 hours and weighed.

After the aerial portion of the shrub was removed, the litter beneath the canopy was collected and screened through a 2-mm screen. The material too coarse to pass through the screen was saved, dried, and weighed. The maximum and minimum diameters of the mound were measured, and the height of the mound was determined by digging to the clay horizon. The number of perennial grasses rooted on the mound was counted by species, and the cover of cheatgrass was estimated ocularly per mound.

A series of age/size classes was established for the black sagebrush plants sampled. These
Table 1. Mean plus standard error (SE) for shrub density per m², percent projected canopy cover, frequency (10-m² plot) within stands (N = 10), and constancy among stands (N = 5).

<table>
<thead>
<tr>
<th>Species</th>
<th>Density (m²)</th>
<th>SE</th>
<th>Cover (%)</th>
<th>SE</th>
<th>Frequency (%)</th>
<th>SE</th>
<th>Constancy (%)</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Artemisia nova</td>
<td>2.2</td>
<td>0.40</td>
<td>22</td>
<td>2.4</td>
<td>100</td>
<td>0</td>
<td>100</td>
<td>0</td>
</tr>
<tr>
<td>Chrysothamnus viscidiflorus</td>
<td>0.7</td>
<td>0.10</td>
<td>2</td>
<td>0.4</td>
<td>40</td>
<td>8</td>
<td>80</td>
<td>8</td>
</tr>
<tr>
<td>Ephedra nevadensis</td>
<td>0.3</td>
<td>0.08</td>
<td>1</td>
<td>0.4</td>
<td>64</td>
<td>10</td>
<td>100</td>
<td>0</td>
</tr>
<tr>
<td>Tetradymia glabrata</td>
<td>0.2</td>
<td>0.04</td>
<td>3</td>
<td>0</td>
<td>32</td>
<td>5</td>
<td>60</td>
<td>4</td>
</tr>
<tr>
<td>Eriogonum microthecum</td>
<td>0.1</td>
<td>0.04</td>
<td>5</td>
<td>0</td>
<td>5</td>
<td>1</td>
<td>20</td>
<td>2</td>
</tr>
<tr>
<td>Eriogonum umbellatum</td>
<td>0.2</td>
<td>0.00</td>
<td>-a</td>
<td>-</td>
<td>-</td>
<td>8</td>
<td>1</td>
<td>20</td>
</tr>
</tbody>
</table>

*a Indicates less than 1% average cover.

classes were based on the size, growth form, percentage dead canopy, and apparent age of the plants. The classes were (a) seedling, (b) young plant, (c) mature plant, (d) patriarch, (e) senescent, and (f) dead.

Soil samples from the surface 5 cm were taken (a) next to the shrub stem, (b) at the canopy edge, and (c) 10 cm beyond the edge of the shrub canopy. These samples were dried, screened, and shipped to a commercial laboratory for nitrate nitrogen analysis.

A two-way analysis of variance and post hoc Duncan's Multiple Range test were performed to analyze differences in soil nitrate concentration between sagebrush age/size classes and sample location. A series of stepwise regressions was performed, utilizing the general linear model, wherein a subset of variables was chosen that would best predict plant weight, annual growth of plant (weight), and leaf weight of black sagebrush. Separate step-up regressions were performed for plant and mound characteristics (Neter and Wasserman 1974). The independent variables that were significant contributors to predicting age/size classes for these two groups were chosen as discriminant variables to be used in two separate discriminant analyses. The age/size classes of the sagebrush plants were used as the grouping structure in the discriminant analysis. The plant characteristic variables selected as significant contributors to classification into age/size classes were (a) weight of coarse stems, (b) number of stems, (c) plant height, and (d) plant diameter. The mound characteristics (ranked in order of importance) used were (a) litter cover, (b) litter weight, (c) soil nitrate concentration, and (d) cheatgrass cover on the mound.

RESULTS AND DISCUSSION

Community Competition

The plant communities of the Buckskin Mountains dominated by black sagebrush are low in diversity (Table 1). Green rabbitbrush (Chrysothamnus viscidiflorus (Hook.) Nutt.) occurs in patches in the community. Nevada ephedra (Ephedra nevadensis Wats.) is rather evenly distributed through the black sagebrush communities, but at a low density. Littleleaf horsebrush (Tetradymia glabrata Gray) is a relatively infrequent component of the communities. The two species of Eriogonum are semiwoody species that also occurred in the most arid black sagebrush communities that Zamora and Tueller (1973) reported.

Squirreltail (Elymus hystrix Scribn.) and cheatgrass are the most frequent herbaceous species (Table 2). The relative frequency of the two species reverses from year to year depending on available moisture for plant growth. Cheatgrass is abundant only in years with adequate moisture during the spring. The density of squirreltail plants remains relatively constant. In dry years, squirreltail is virtually the only herbaceous species in these communities.

Biomass

Along the western margin of the Buckskin Mountains, black and basin big sagebrush communities occur side by side on sharply contrasting soils. The basin big sagebrush communities have been burned in wildfires, based on historic records and fire scar analysis (Young et al. 1989). Our analysis of black sagebrush communities is essentially based on aboveground woody material accumulation of the dominant shrub. We had previously conducted a study of the biomass
of basin big sagebrush adjacent to the western edge of the Buckskin Mountains (Young et al. 1989). This allowed comparison of the production of biomass of basin and black sagebrush from the same area. The basin big sagebrush community had a sandy loam surface soil and a greater soil depth (Haplagrids derived from metavolcanic sources). Big sagebrush ages were clumped at 55–60, 40–45, and 10–15 years old.

The general aspect of the two communities is strikingly different, with the maximum height of the black sagebrush being 60 cm and that of the big sagebrush over 1 m. In contrast to the central woody stems of the big sagebrush plants, black sagebrush plants appear multi-stemmed. Despite the difference in height, the two communities have similar biomass because of the higher density of plants in the black sagebrush community. There is more coarse and fine woody material in the basin big sagebrush community (Table 3).

If we assume both populations are the same age (assumption is necessary because actual age of black sagebrush plants could not be estimated), the rate of woody biomass accumulation was 13.2 g/m²/year and 64.5 g/m²/year for black and basin big sagebrush, respectively. The wide difference between the two communities is apparently due to the higher woody biomass of more mature basin big sagebrush plants.

Woody biomass of black sagebrush was best predicted by the equation:

\[ Y = 9.87 + 1.21 \cdot X_1 + 1.12 \cdot X_2 + 0.88 \cdot X_3 \]

where \( Y \) = total woody biomass (grams), \( X_1 \) = fine stems, \( X_2 \) = coarse stems, and \( X_3 \) = root crown. \( R^2 = .96 \) for this determination. Yearly growth increment was predicted by the equation:

\[ Y = 16.96 + 0.26 \cdot X_1 + 0.16 \cdot X_2 - 0.73 \cdot X_3 - 0.14 \cdot X_4 \]

where \( Y \) = current growth, \( X_1 \) = fine stems, \( X_2 \) = coarse stems, \( X_3 \) = plant height, and \( X_4 \) = root crown. \( R^2 = .57 \) for this determination, despite the inclusion of a fourth variable. Our third equation predicted leaf weight:

\[ Y = 23.53 + 0.29 \cdot X_1 - 0.93 \cdot X_2 + 0.2 \cdot X_3 - 0.35 \cdot X_4 \]

where \( Y \) = leaf weight, \( X_1 \) = coarse stems, \( X_2 \) = height of plant, \( X_3 \) = fine stems, and \( X_4 \) = plant density. These four variables in the equation accounted for 64% of the variability in the data.
The selected variables for both plant and mound characteristics were important contributors in distinguishing between age/size classes and were good indicators of group composition (Fig. 1). Very few misclassifications occurred by use of the resulting discriminant functions.

The bulk of the black sagebrush stands was composed of mature plants 20–60 cm tall with canopies 20–50 cm in diameter (Table 4). This is a wide range in height and canopy size, but the mature age/size class was distinguished from young plants by the presence of up to 10% dead material in the canopy and the beginning of the separation of the stem into individual cambium bundles. The patriarch class was distinguished from the mature class by an increase in dead material in the canopy (to 30%) and complete separation of the stems. The separated stems formed U-shaped flutes with the open end of the U toward the former center of the stem. It was not possible to establish the maximum age of the class because the center of the stem was missing. The individual section had at least 40 growth rings.

Senescent plants formed the next, apparently older, age/size class. In this class at least 50% of the canopy was dead. Older black sagebrush plants do not get taller, probably because they have no central stem to support the canopy. The diameter of the crowns does increase. There is a marked increase in woody biomass between the patriarch and senescent classes.

Seedlings and young plants constituted only 6% of the black sagebrush populations (Table 4),
Table 3. Mean density (STEMS/m²) plus standard error (SE) and oven-dry biomass (g/m²) of Artemisia nova and A. tridentata subsp. tridentata. Data for A. tridentata subsp. tridentata from a previous study (Young et al. 1989).

<table>
<thead>
<tr>
<th>Species</th>
<th>Density</th>
<th>Coarse</th>
<th>Fine</th>
<th>CAG</th>
<th>Leaves</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>m²</td>
<td>g</td>
<td>g</td>
<td>g</td>
<td>g</td>
<td>g</td>
</tr>
<tr>
<td>Artemisia nova</td>
<td>2.2</td>
<td>0.4</td>
<td>750</td>
<td>90</td>
<td>520</td>
<td>60</td>
</tr>
<tr>
<td>Artemisia tridentata</td>
<td>1.1</td>
<td>0.3</td>
<td>850</td>
<td>100</td>
<td>970</td>
<td>110</td>
</tr>
</tbody>
</table>

Table 4. Artemisia nova crown and biomass characteristics for individual age/size classes. Demographic breakdown of black sagebrush communities by growth classes. Classes are related to age for younger plants, but once stems separate, ages are not based on annual rings.

<table>
<thead>
<tr>
<th>Age/size Class</th>
<th>Height (cm)</th>
<th>Diameter (cm)</th>
<th>Density (%</th>
<th>Dead branches (%)</th>
<th>Coarse stems (g)</th>
<th>Fine stems (g)</th>
<th>CAG (g)</th>
<th>Leave (g)</th>
<th>Stem number</th>
<th>Percentage of stand</th>
<th>Age (years)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Seedling</td>
<td>5</td>
<td>5</td>
<td>30</td>
<td>0</td>
<td>0</td>
<td>5</td>
<td>10</td>
<td>1</td>
<td>&gt;1</td>
<td>2-5</td>
<td></td>
</tr>
<tr>
<td>Young plant</td>
<td>10-20</td>
<td>5-10</td>
<td>50</td>
<td>0</td>
<td>25</td>
<td>46</td>
<td>40</td>
<td>1</td>
<td>5</td>
<td>5-30</td>
<td></td>
</tr>
<tr>
<td>Mature</td>
<td>20-60</td>
<td>10-50</td>
<td>80</td>
<td>10</td>
<td>140</td>
<td>120</td>
<td>80</td>
<td>60</td>
<td>Multiple</td>
<td>60</td>
<td>30-50</td>
</tr>
<tr>
<td>Patriarch</td>
<td>20-60</td>
<td>20-80</td>
<td>60</td>
<td>30</td>
<td>560</td>
<td>420</td>
<td>140</td>
<td>100</td>
<td>Multiple</td>
<td>17</td>
<td>40+</td>
</tr>
<tr>
<td>Senescent</td>
<td>20-60</td>
<td>20-100</td>
<td>30</td>
<td>60</td>
<td>980</td>
<td>640</td>
<td>60</td>
<td>30</td>
<td>Multiple</td>
<td>12</td>
<td>?</td>
</tr>
<tr>
<td>Dead</td>
<td>20-60</td>
<td>20-100</td>
<td>0</td>
<td>100</td>
<td>910</td>
<td>320</td>
<td>0</td>
<td>0</td>
<td>Multiple</td>
<td>5</td>
<td>?</td>
</tr>
</tbody>
</table>

with seedlings being very rare. The separation between seedling and young plants was based on the occurrence of coarse, woody biomass in the latter class. Young plants had entire stems with no evidence of division of the cambium.

Mound Types

Each black sagebrush age/size class had a corresponding type of sub-canopy mound. The only seedling found in the entire study was located in an interspace between mounds. Obviously, one seedling is not a valid sample, but the lack of seedlings is a critical factor in the dynamics of the communities studied. The first detectable mound occurred under young plants. Only 5-10% of the sub-canopy area under black sagebrush plants in the young plant age/size class was covered with litter (Table 5). The litter was composed of fragments of black sagebrush leaves.

In the mature plant age/size class the cover of litter and the weight of litter increased (Table 5). The mounds were easily distinguished by both height and surface soil color and texture. The surface of the mounds appeared darker in color, and the reddish tinge to the clay surface soils of the interspace was not apparent. If the surface of the mound was disturbed, the dark color was replaced by a grayish shade. Mounds appear to reach their maximum height with this growth stage of black sagebrush. Mounds of mature plants had perennial grasses associated with the sub-canopy area. The most frequent perennial grass was squirrel tail.

Litter accumulations increased with the patriarch age/size class, but height of the mound did not increase. Apparently, trapping of subaerial deposition material and saltation particles must be related to growth stage of black sagebrush plants in terms of crown architecture. Subaerially deposited particles are obviously very unstable and subject to redeposition if they fall in the largely bare interspace among shrub mounds (Young and Evans 1986). If litter accumulation increases on patriarch mounds, why do they not trap these secondary erosion products and the mound keep growing in height? Canopy structure changes with the patriarch age/size class, with increasing bare stems and spreading, but not taller, plants. It would appear that aerial dynamics of the crown of black sagebrush plants influence mound height.

With the senescent age/size class, a divergence
in herbaceous species composition on the mounds occurs (Table 5). Some mounds become densely covered with cheatgrass as black sagebrush plants become senescent and others support colonies of squirreltail.

After the black sagebrush plants die, litter weight continues to increase and litter changes in appearance. Litter under dead plants is composed of stringy bark fragments, and individual black sagebrush leaves cannot be distinguished in the litter.

**Soil Nitrate Levels**

Surface soil nitrate levels were higher beneath shrub canopies than in the interspace (Table 6). Levels were highest next to shrub stems. Nitrate levels beneath the canopy rose as age/size classes of black sagebrush indicated older plants and mounds. This is in itself an indication that age/size classes actually do reflect increasing age. The development of vertical and horizontal patterns in soil nitrogen, attributed to the localization of litter fall beneath the canopies of desert shrubs, has been documented by the research of N. E. West and co-workers (Charley and West 1977, West and Skujins 1977, West 1979). Nitrate levels of surface soils dropped significantly \( P \leq 0.01 \) once the black sagebrush plants died. Nitrate levels in surface soils at the edge of shrub mounds increased with apparent increasing age of black sagebrush plants and mounds. These areas correspond to the micro-topoedaphic situation described as coppice benches by Eckert et al. (1989) for shrub mounds in big sagebrush communities. Apparently the increase in soil nitrate results from leaching from the mounds. Once black sagebrush plants are dead and grasses dominate the mound, soil nitrate levels decrease.

**Mounds and Black Sagebrush Community Structure**

We did not find grass-dominated mounds or grass-dominated mounds with black sagebrush seedlings. We did note the remains of mounds that appeared to be eroding away. Apparently,
mounds are dynamically formed and eroded in relation to the establishment and eventual death of black sagebrush plants. The failure to find grass-dominated mounds may be a function of herbivory by domestic livestock [sheep, feral horses (Equus caballus), and black-tailed jackrabbits (Lepus californicus)]. Grass-dominated mounds may fail to persist since grasses cannot maintain mounds because of leaf fall and canopy structure differences compared with black sagebrush plants. The only patchy vegetation encountered in the communities was groups of rabbitbrush plants. Perhaps rabbitbrush increases after relatively short-lived squirreltail plants die or are reduced by grazing. In an adjacent big sagebrush community we previously determined three episodes of seeding establishment at 12, 42, and 57 years before 1985 (Young et al. 1989). Plant ages were clustered around these apparent establishment dates. The clusters may represent periods of desirable climate for seeding establishment or a single season when establishment occurred; they may also represent variability in growth ring deposition or recognition. The classes we constructed in this study are much too broad to pinpoint this type of episodic stand establishment for black sagebrush. Perhaps black sagebrush communities not renewed catastrophically by wildfires only require stand renewal at such low levels (5% of the stand, standing dead plants) that our one seedling sampled is sufficient for community regeneration.

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