VIEW Points

Sagebrush, Common and Uncommon, Palatable and Unpalatable By E. Durant McArthur

read with interest Jim Brunner's recent view point article¹ where he briefly traced the recognition of palatable forms of sagebrush. Jim's keen sense of differences in sagebrush taxa were first published more than 3 decades ago.² Jim's comments stimulated some thoughts of my own about the recognition, distribution, and palatability of sagebrush taxa. I'm sharing some of those thoughts here.

Sagebrush is an icon of the American West.³ However, it is a symbol that stirs a range of emotions among rangeland managers.^{4–7} An appreciation for the values of sagebrush ecosystems has been a long time coming and, unfortunately, is juxtaposed with a fragmentation of that resource over much of its historic range.^{4,5} That is not to say that there are areas that may not need management, including reduction of sagebrush density, but more often, in my opinion, the weightier need is for restoration and enhancement.

Sagebrush ecosystems are varied and rich in indigenous and multitudinous forms of life. Some forms are obligate to their sagebrush habitat, eg, greater sage-grouse, Gunnison sage-grouse, pygmy rabbits, sage thrasher, and sage sparrow.^{4,5}

Brunner¹ pointed out that sagebrush is diverse in form and in its acceptance as forage for animals (palatability). Some taxa are common; others are not. Big sagebrush is the central and most important species to the group that forms its own portion of the large genus Artemisia-the subgenus Tridentatae (Table 1). This group is composed of wholly western North American endemics, although Artemisia in general, through representation of its other subgenera, occurs widely around the world. I believe there are 6 kinds (subspecies) of big sagebrush. Three of these are common throughout the distributional range of the subgenus and species, which is nearly the same. The geographic range of the subgenus is only slightly larger than that of big sagebrush itself, to the northeast by silver sagebrush (Artemisia cana) and to the southeast by Bigelow sagebrush (A. bigelovii).8 The common subspecies are basin, mountain, and Wyoming

big sagebrushes, respectively, the subspecies tridentata, vaseyana, and wyomingensis. These subspecies each have distinctive morphological differences and habitat preferences but can be distributed in close proximity.9 The distribution of basin big sagebrush in particular is highly fragmented because the deep, well-drained soils that it prefers are prime agricultural and urban lands. Mountain big sagebrush is sometimes divided into 2 varieties based on the number of flowers per head. The common mountain big sagebrush east of the Cascade-Sierra axis is sometimes termed variety pauciflora to contrast it with the plants with larger flower heads that occur at higher elevations and latitudes (variety vaseyana of ssp. vaseyana). Both are quite similar, and I am comfortable in calling both "mountain big sagebrush." The recognition of Wyoming big sagebrush has expanded widely during my career. It was not described until 1965.10 I well remember my introduction to bona fide Wyoming big sagebrush. It was at the field trip of the 1973 Wyoming Shrub Ecology Workshop held in Pinedale. Alan Beetle, who with his student Alvin Young had described the subspecies, led the field trip to the type location. Before that time, my experience with what I thought was Wyoming big sagebrush had been with what has subsequently been formally described as Lahontan low sagebrush (A. arbuscula ssp. longicaulis).¹¹ My mentor Perry Plummer had many accessions of sagebrush growing at the Snow Field Station in Ephraim, Utah, among which were accessions of Lahontan low sagebrush, which had been collected as seedling transplants from northwestern Nevada as "widelobe" with the sobriquet "an ecotype of Wyoming big sagebrush" from Alan Beetle through Jim Brunner. After I had learned what typical Wyoming big sagebrush was really like at the Wyoming Shrub Ecology Workshop, I saw that it was widely distributed, but previously unrecognized, in many locations. Others have recognized this wide distribution as well; published studies recognize it in 11 states.^{12,13} It is always tetraploid (has 4 sets of chromosomes), whereas basin and mountain big sagebrush are usu-

Table 1. Sagebrush (subgenus Tridentatae) taxa (species and subspecies) with their general distributions and site adaptation

Species	Subspecies	Distribution and site adaptation
Low sagebrush (<i>Artemesia</i> <i>arbuscula</i>)	Low sagebrush (<i>arbuscula</i>)	W WY to S central WA and N CA on dry sterile, rocky, shallow, alkaline, clay soils
	Cleftleaf sagebrush (thermopola)	W WY, N UT, and E ID on spring-flooded, summer- dry soils
	Lahontan low sagebrush (<i>longicaulis</i>)	NW NV extending into adjacent CA, OR, and ID on soils of low water-holding capacity and shallow depth usually around and above the old shoreline of Lake Lahontan
Coaltown sagebrush (A. argillosa)		Jackson County, CO on alkaline spoil material
Bigelow sagebrush (A. bigelovii)		Four-corners area extending to NE UT, SE CA, and W TX on rocky, sandy soils
Silver sagebrush (<i>A. cana</i>)	Bolander silver sagebrush (<i>bolanderi</i>)	E OR, W NV, and N CA in alkaline basins
	Plains silver sagebrush (<i>cana</i>)	Generally E of Continental Divide, Alberta, and Manitoba to CO on loamy to sandy soils of river and stream bottoms
	Mountain silver sagebrush (<i>viscidula</i>)	Generally W of Continental Divide, MT, and OR to AZ and NM in mountain areas along streams and in areas of heavy snowpack
Alkali sagebrush (<i>A. longiloba</i>)		SW MT, NW CO, W WY, N UT, S ID, N NV, and E OR on heavy soils derived from alkaline shales or on lighter, limey soils
Black sagebrush (<i>A. nova</i>)	Black sagebrush (<i>nova</i>)	SE OR and S central MT to S CA and NW NM on dry, shallow, stony soils with some affinity for cal- careous conditions
	Duchesne black sagebrush (<i>duchesnicola</i>) [†]	NE UT on reddish clay soils of Duchesne River Formation
Pygmy sagebrush (<i>A. pygmaea</i>)		Central NV and NE UT to N AZ on calcareous desert soils
Stiff sagebrush (A. rigida)		E OR, W central ID, and E WA on rocky scablands
Rothrock sagebrush (A. rothrockii)		E CA and W NV on deep soils along forest and meadow margins in Sierra Nevada and outlying mountain ranges
Big sagebrush (<i>A. tridentata</i>)	Parish big sagebrush (<i>parishii</i>)	Los Angeles basin area on deep soils in chaparral and saltbush habitats
	Snowbank big sagebrush (<i>spiciformis</i>)	WY, ID, CO, and UT in high mountains associated with A. cana ssp. viscidula but in slightly drier areas
	Basin big sagebrush (<i>tridentata</i>)	BC and MT to NM and Baja CA in dry, deep, well- drained soils on foothills and mountains
	Mountain big sagebrush (<i>vaseyana</i>)	BC and MT to S CA and N NM in deep, well- drained soils on foothills and mountains
	Wyoming big sagebrush (<i>wyomingensis</i>)	ND and WA to AZ and NM on shallower well- drained soils often underlain by a caliche or silica layer in valleys and on foothills
	Xeric big sagebrush (<i>xericensis</i>)	W central ID on basaltic and granitic soils

Table 1. Continued		
Species	Subspecies	Distribution and site adaptation
Threetip sagebrush (A. tripartita)	Wyoming threetip sagebrush (<i>rupicola</i>)	W and S WY on rocky knolls
	Tall threetip sagebrush (<i>tripartita</i>)	E WA and W MT to N NV and N UT on moderate- to-deep well-drained soils
[†] Duchesne black sagebrush has been described at the variety level, but its rank is parallel to the subspecies of this treatment. Sources: Modified from McArthur 1994 ³⁴ and Mahalovich and McArthur 2004 ⁸ and references cited therein.		

ally diploid.¹² Subsequent work in collaboration with Alma Winward led us to formally describe the wide-lobe taxon as *Artemisia arbuscula* ssp. *longicaulis*,¹¹ which is likely a stabilized hybrid between typical Wyoming big sagebrush and typical low sagebrush. It, *A. arbuscula* ssp. *longicaulis* or Lahontan low sagebrush, combines morphological, chemical, and cytological features of the 2 putative parents (the flowers of low sagebrush, and a combined hexaploid genome or chromosome complement).¹¹ Lahontan low sagebrush is a palatable taxon. It is often hedged. It has a relatively limited distribution—northwestern Nevada spilling into adjacent California and Oregon.¹¹

The 3 other subspecies of big sagebrush that I recognize are of limited distribution. These are spicate or snowbank big sagebrush, ssp. spiciformis; xeric big sagebrush, ssp. xericensis; and Parish big sagebrush, ssp. parishii. Spicate big sagebrush is a high-elevation taxon of the Intermountain area, of probable hybrid ancestry (mountain big sagebrush × mountain silver sagebrush) that was formerly confused with Rothrock sagebrush.¹⁴ Rothrock sagebrush (A. rothrockii) is also a highelevation taxon but is limited to the Sierra Nevada and its outlier mountains and is a high polyploid, with hexaploid and octoploid populations, whereas spicate big sagebrush is diploid and tetraploid.¹² Xeric big sagebrush is limited in its distribution to west central Idaho; it is a tetraploid taxon derived from putative diploid ancestors, basin (A. tridentata ssp. tridentata) and mountain (A. tridentata ssp. vaseyana)^{12,15} big sagebrush. In other places, basin big sagebrush and mountain big sagebrush have formed hybrid swarms without stabilizing into new polyploid taxa as they apparently did in the case of xeric big sagebrush.¹⁶ Parish big sagebrush is a narrow endemic that occurs only in the Los Angles basin area of southern California. I had been inclined not to recognize it as a distinct taxon because it is similar to basin big sagebrush. However, I recently examined several natural populations. Its populations have distinctive, bimodal phenotypes with upright and droopy inflorescences and soft, pliable vegetative branches as opposed to the stiffer ones of the basin big sagebrush. In addition, these large, robust plants are tetraploid, whereas the large-basin big sagebrush are diploid.^{12,17,18} The suggestion by Beetle¹⁹ and Brunner¹ that

Parish big sagebrush is widespread beyond the Los Angeles basin is, I believe, erroneous. Table 1 lists the general distributions and adaptation of sagebrush taxa.

Individual taxa have become established over geological time as populations filled niches made available through climatic, edaphic, and other environmental variables. These taxa were able to differentiate, I believe, through the processes of isolation and selection with new combinations made possible through hybridization and polyploidy, both of which are important in the Tridentatae. 12,16,20 Several extant Tridentatae taxa are thought to be of hybrid origin.^{11,16,20} In many places, different taxa occur sympatrically or very close to one another. Hybridization can occur in these areas, although strong selection and ploidy (chromosome number) differences usually preclude speciation.¹⁶ Winward²¹ has suggested a rather widespread set of populations that he calls informally A. tridentata hybrid B (Bonneville big sagebrush), which occupy habitats between mountain and Wyoming big sagebrush and which might, in fact, be a distinct taxon. I and some colleagues^{12,16,22} have argued that these populations might best be viewed as Wyoming big sagebrush that have been introgressed by mountain big sagebrush. All of these populations that have been examined cytologically share the tetraploid condition of Wyoming big sagebrush.^{12,18}

As landscape-dominant plants, sagebrushes are important as the host organism and as habitat for many associated species, including species of special concern such as sage grouse, pygmy rabbit, sage thrasher, sage sparrow, Brewer's sparrow, and raptor species.^{4,5,23} The relative palatability of sagebrush species to domestic livestock and wild ungulates generates much of the contrasting judgment by rangeland managers of its value on landscapes. Whereas it is not eaten much by cattle; mule deer, elk, domestic sheep, and antelope consume large quantities of sagebrush.^{4,24–28} Individual populations, subspecies, and species have been shown to be preferred by different consuming animal species under both natural and controlled conditions. For example, studies have shown that:

• Mule deer prefer mountain big sagebrush and low sagebrush to basin and Wyoming big sagebrush and black sagebrush.^{25,27,28}

- Greater sage-grouse prefer mountain big sagebrush to basin and Wyoming big sagebrush.²⁹
- Domestic sheep preferred Wyoming big sagebrush to mountain and basin big sagebrush in one study²⁶ but preferred low sagebrush and black sagebrush to other taxa in another study.²⁸
- Lahontan low sagebrush is a preferred taxon by browsing animals. $^{1,2,30}\!\!$
- Black sagebrush (*A. nova*) is palatable in many circumstances to domestic sheep, antelope, and mule deer although often less palatable than big sagebrush.^{27,28,31-33}

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