

SAGEBRUSH SYSTEMATICS AND DISTRIBUTION

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INTRODUCTION

In this paper on sagebrush systematics and distribution, it is appropriate to begin by defining a few terms. Sagebrush, under my definition, are woody North American *Artemisia* of the subgenus *Tridentatae*. *Tridentatae* are one of four subgenera in *Artemisia*. *Tridentatae* or true sagebrush are separated from other *Artemisia* of the subgenera *Artemisia*, *Dracunculus*, and *Seriphidum* (e.g., wormwood, wormseed, sage, tarragon, etc.) by their completely woody nature, exclusive North American distribution, distinctive chemistry and molecular genetics, and their fertile, homogamous, perfect disc flowers (McArthur 1979, McArthur and Sanderson 1999a). There are 11 sagebrush species that, together with their subspecific entities, account for about 20 taxa. *Artemisia* as a whole includes more than 200 species.

We define systematics following Judd et al. (1999): systematics is the science of organismal diversity which entails the discovery, description, and interpretation of biological diversity as well as the synthesis of information in the form of predictive classification systems. According to Judd et al. (1999) the aim of systematics is to discover the branches of the tree of life, to document the changes that have occurred during the evolution of these branches, and to describe taxa (usually species) at the tips of these branches.

Distribution, of course, is the natural geographic range of organisms. For sagebrush taxa, there is a distribution of the whole group and subset distributions of taxa that constitute sagebrush which may be sympatric (occurring in the same area), parapatric (occurring in separate but adjoining areas), and allopatric (occurring in different areas).

SAGEBRUSH SYSTEMATICS

Artemisia is a distinguished name, an etymological descendant of an early Mother Nature. Artemis was the ancient Greek goddess of wild animals, the hunt, and vegetation, and of chastity and childbirth (McArthur 1979). *Tridentatae* and *tridentata* both refer to the characteristic three lobes of many sagebrush taxa.

Subgenus *Tridentatae* of *Artemisia* is a group of plants centered on the landscape-dominant *A. tridentata*

complex. There have been several systematic treatments of the group (see Kornkven et al. 1998 and McArthur et al. 1998a for recent reviews). My colleagues and I (McArthur et al. 1998a, McArthur and Sanderson 1999a) recognize 11 species and 14 subspecies (Table 1). *Artemisia* is centered, in distribution and diversity, on the great Eurasian landmass. There is compelling distributional, chemical, and genetic evidence that North American *Tridentatae* are derived from Eurasian stock and that they differentiated and expanded during Pliocene and Pleistocene with the changing climates and habitats of those epochs (summarized in McArthur et al. 1998a,b; McArthur and Sanderson 1999a).

Differentiation and evolution within *Tridentatae* has been facilitated by polyploidy and hybridization. All the major species (big sagebrush [*A. tridentata*], silver sagebrush [*A. cana*], low sagebrush [*A. arbuscula*], and black sagebrush [*A. nova*]), as well as several less common or more geographically restricted ones (Bigelow sagebrush [*A. bigelovii*] and Rothrock sagebrush [*A. rothrockii*]), include both diploid and polyploid populations (Table 2). Based on habitat occupation, we have hypothesized that polyploidy is adaptive, i.e., polyploid populations are usually found in drier habitats than are related diploids (Sanderson et al. 1989, McArthur and Sanderson 1999a). Polyploids are smaller with slower growth rates that make them better adapted to drier conditions (Sanderson et al. 1989).

Some species have poorer support for taxonomic placement in *Tridentatae* than others. Bigelow sagebrush has floral anomalies, and pygmy sagebrush (*A. pygmaea*) has morphological anomalies; but both have karyotypic and molecular genetic characteristics of *Tridentatae*. There is evidence that sand sage (*A. filifolia*), ordinarily placed in subgenus *Dracunculus*, has some affinities with subgenus *Tridentatae* based on chloroplast DNA, plant chemistry, and chromosomal karyotype (Kornkven et al. 1998, McArthur and Sanderson 1999a). An anomalous plant, *A. palmeri*, is wholly herbaceous but has the floral formula of *Tridentatae*; however, I follow Rydberg (1916) and exclude it from *Tridentatae*.

Hybridization is common in this group and has apparently been a mechanism providing new genetic combinations to facilitate occupation of changing habitats during the evolutionary history of *Tridentatae* (Ward 1953, McArthur et al. 1988, McArthur and Sanderson

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1999a). In a series of studies (reviewed by Graham et al. 1999 and McArthur and Sanderson 1999b), my colleagues and I have examined a narrow hybrid zone between basin (*A. tridentata* ssp. *tridentata*) and mountain (*A. t.* ssp. *vaseyana*) big sagebrush. We have studied adaptation, growth, gene flow, chemistry, physiology, soils, mineral distribution and uptake, and plant and animal communities across the zone and in reciprocally transplanted gardens. We concluded that hybrids are adapted to these zones and that points of contact between differentiated taxa (hybrid zones) could have been the source for differentiation of new genetic combinations. These combinations were able to exploit new habitats associated with changing climates of the Pliocene and Pleistocene Epochs, continuing until the present. Several extant *Tridentatae* species, subspecies, and populations, described and undescribed, are of hybrid origin, e.g., Lahonton low sagebrush (*A. arbuscula* ssp. *longicaulis*), spicate or snowbank big sagebrush (*A. tridentata* ssp. *spiciformis*), and xeric big sagebrush (*A. tridentata* ssp. *xericensis*) (Winward and McArthur 1995, McArthur and Sanderson 1999b). Artificial hybridization may be useful for management purposes in selecting and combining traits in sagebrush for palatability, nutritive quality, and fire tolerance (McArthur et al. 1988, McArthur et al. 1998a).

SAGEBRUSH DISTRIBUTION

Artemisia in general is widely distributed throughout the northern hemisphere with disjunct distribution to some, mainly mountainous, southern hemisphere locations (Good 1974). However, the subgenus *Tridentatae* is wholly western North American (Fig. 1). West of the 100° west longitude at mid-latitudes, sagebrush is a dominant, widely distributed plant (Fig. 1, Table 1). Figure 1 illustrates aspects of the group's distribution, including the wide distribution of the central species, big sagebrush. Big sagebrush, with its subspecies, extends over most of the geographic range covered by the subgenus as a whole. The nature of areas dominated by sagebrush is also illustrated in the figure, using the state of Utah as an example. Large areas are dominated by sagebrush, but some of its species are less significant components of other communities, e.g., mountain brush and pinyon-juniper. However, some taxa, e.g., pygmy

sagebrush, Bigelow sagebrush, Alkali sagebrush (*A. longiloba*), and stiff sagebrush (*A. rigida*), grow in specific, limited habitats.

Sagebrush taxa grow at elevations and precipitation levels above the salt desert shrub communities, i.e., precipitation above 18-20 cm per year. For the common big sagebrush subspecies in the Intermountain area, the annual precipitation levels are: about 32-36 cm for basin big sagebrush (however, basin big sagebrush often grows in areas that benefit from seasonally high water tables at different precipitation levels), about 20-30 cm for Wyoming big sagebrush (*A. t.* ssp. *wyomingensis*), and generally above 30 cm for mountain big sagebrush (Monsen and McArthur 1984, Goodrich et al. 1999).

General distribution and site conditions for each species and subspecies are presented in Table 1. Distribution of sagebrush species and subspecies is usually associated with specific soil properties and soil parental material as well as climatic differences (Passey et al. 1982, Wang et al. 1998, Wang et al. 1999). Seed recruitment conditions are generally tied to local climatic conditions, i.e., seeds germinate and establish better in habitats climatically like those that produced them (Meyer and Monsen 1992).

There is a high incidence of parapatric and sympatric distribution within *Tridentatae*. Many taxa, however, have allopatric distributions with regard to one another (Table 1). This type of distribution pattern, together with wind pollination, facilitates hybridization within the group. However, despite hybridization and the occurrence of hybrid zones, most populations and individuals are clearly assignable to parental taxa (Beetle 1970).

Unfortunately, sagebrush ecosystems have been badly disturbed (intensive grazing, introduction of cheatgrass, etc.) beyond historic natural disturbance cycles, as witnessed by other contributions in this symposium and by previous works, e.g., Passey et al. (1982) and contributions in Monsen and Kitchen (1994). I believe integrity and maintenance of sagebrush communities is important for healthy, naturally functioning ecosystems on a continental scale, as many other components of sagebrush ecosystems are dependent on this keystone species.

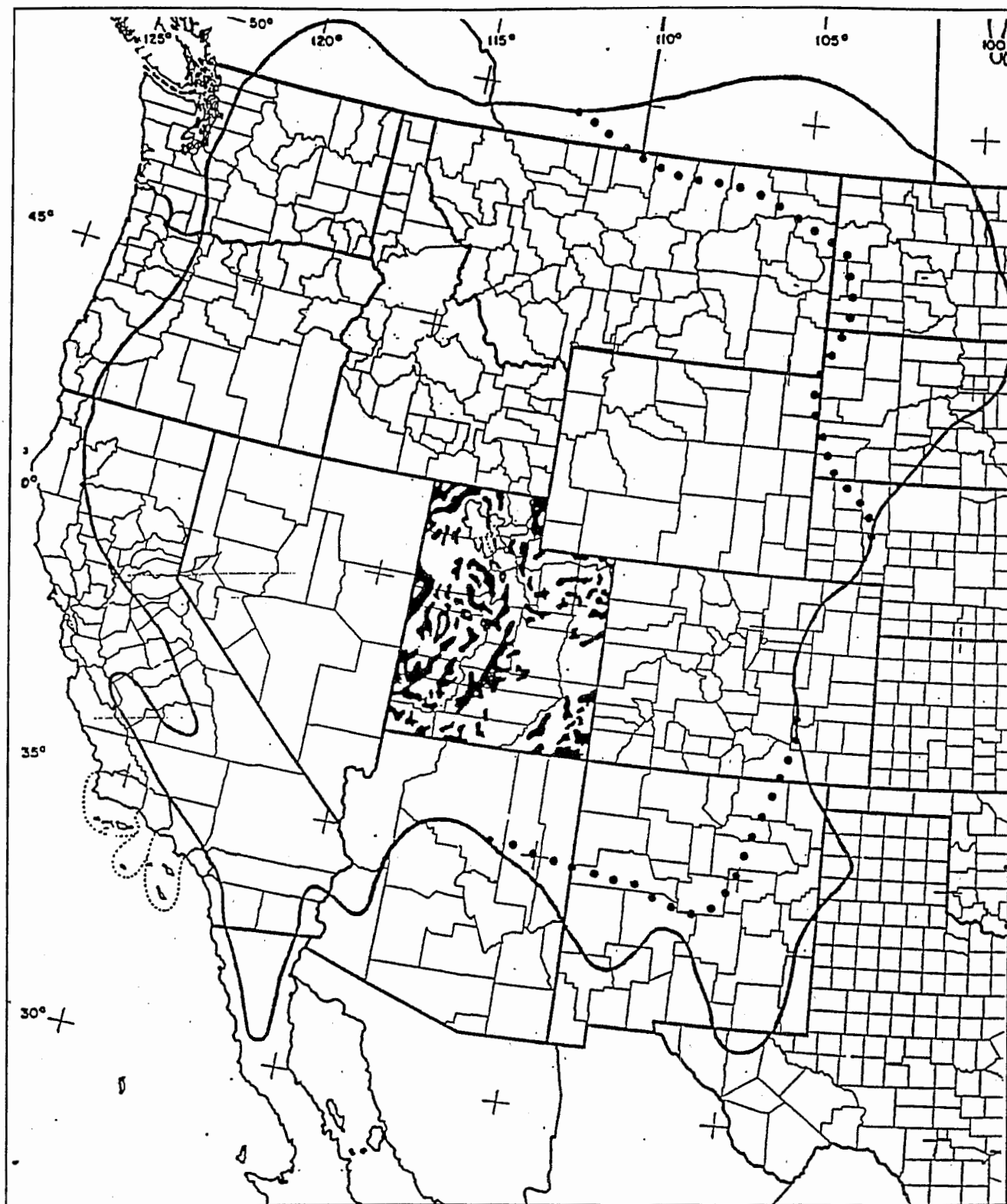


Figure 1. Distribution of sagebrush (subgenus *Tridentatae* of *Artemisia*). Solid line is the extent of distribution. Dotted lines delineate areas where *A. tridentata* doesn't grow; the northeast extension reflects the distribution of *A. cana*, and the southeast extension reflects the distribution of *A. bigelovii*. Solid black areas are zones of sagebrush dominance in Utah (from McArthur 1979).

Table 1. Sagebrush (subgenus *Tridentatae*) taxa (species and subspecies) with their general distributions and site adaptation (after McArthur 1994 with additions from Winward and McArthur 1995 and Welsh and Goodrich 1995).

<u>Species</u>	<u>Subspecies</u>	<u>Distribution and Site Adaptation</u>
Low sagebrush (<i>A. arbuscula</i>)	Low sagebrush (<i>arbuscula</i>)	W. Wyoming to S.C. Washington and N. California on dry, sterile, rocky, shallow, alkaline, clay soils.
	Cleftleaf sagebrush (<i>thermopola</i>)	W. Wyoming, N. Utah, and E. Idaho on spring-flooded, summer-dry soils.
	Lahontan sagebrush (<i>longicaulis</i>)	N.W. Nevada extending into adjacent California and Oregon on soils of low water-holding capacity and shallow depth, usually around and above the old shoreline of Lake Lahontan.
Coaltown sagebrush (<i>A. argillosa</i>)		Jackson County, Colorado, on alkaline spoil material.
Bigelow sagebrush (<i>A. bigelovii</i>)		Four Corners area extending to N.E. Utah, S.E. California, and W. Texas on rocky, sandy soils.
Silver sagebrush (<i>A. cana</i>)	Bolander silver sagebrush (<i>bolanderi</i>)	E. Oregon, W. Nevada, and N. California on alkaline basins.
	Plains silver sagebrush (<i>cana</i>)	Generally E. of Continental Divide, Alberta and Manitoba to Colorado on loamy to sandy soils of river bottoms.
	Mountain silver sagebrush (<i>viscidula</i>)	Generally W. of Continental Divide, Montana and Oregon to Arizona and New Mexico in mountain areas along streams and in areas of heavy snowpack.
Alkali sagebrush (<i>A. longiloba</i>)		S.W. Montana, N.W. Colorado, W. Wyoming, N. Utah, S. Idaho, N. Nevada, and E. Oregon on heavy soils derived from alkaline shales or on lighter, limey soils.
Black sagebrush (<i>A. nova</i>)	Duchesne black sagebrush (<i>duchesnicola</i>) ^a	Uinta Basin, Utah, in reddish clay soil uplands.
	Black sagebrush (<i>nova</i>)	S.E. Oregon and S.C. Montana to S. California and N.W. New Mexico on dry, shallow, stony soils, with some affinity for calcareous conditions.
Pygmy sagebrush (<i>A. pygmaea</i>)		C. Nevada and N.E. Utah to N. Arizona on desert calcareous soils.
Stiff sagebrush (<i>A. rigida</i>)		E. Oregon, E. Washington, and W.C. Idaho on rocky scablands.
Rothrock sagebrush (<i>A. rothrockii</i>)		California and Nevada in deep soils along the forest margins of the Sierra Nevada and outliers.

(Continued)



Table 1 (cont.)

<u>Species</u>	<u>Subspecies</u>	<u>Distribution and Site Adaptation</u>
Big sagebrush (<i>A. tridentata</i>)	Snowbank big sagebrush (<i>spiciformis</i>)	Wyoming, Idaho, Colorado, and Utah in high mountains.
	Basin big sagebrush (<i>tridentata</i>)	British Columbia and Montana to New Mexico and Baja California in dry, deep, well-drained soils on plains, valleys, and foothills.
	Mountain big sagebrush (<i>vaseyana</i>)	British Columbia and Montana to Baja California in dry, deep, well-drained soils on foothills and mountains.
	Wyoming big sagebrush (<i>wyomingensis</i>)	North Dakota and Washington to Arizona and New Mexico in poor shallow soils often underlain by a caliche or silica layer.
	Xeric big sagebrush (<i>xericensis</i>)	W.C. Idaho on basaltic and granitic soils.
Threetip sagebrush (<i>A. tripartita</i>)	Wyoming threetip sagebrush (<i>rupicola</i>)	Wyoming on rocky hills.
	Tall threetip sagebrush (<i>tripartita</i>)	E. Washington and W. Montana to N. Nevada and N. Utah on moderate-to-deep well-drained soils

^aDescribed at the variety level by Welsh and Goodrich (1995) but analogous to the other subspecies listed in the table.

Table 2. Summary of subgenus *Tridentatae* chromosome counts (after McArthur and Sanderson 1999a).

Species	No. ssp. ^a	No. pops.	No. plants	<u>2x</u>	No. pops. ^b at		
					<u>4x</u>	<u>6x</u>	<u>8x</u>
<i>Artemisia arbuscula</i> ^b	2	51	139	25	18	8	0
<i>Artemisia argillosa</i>	1	1	4	0	1	0	0
<i>Artemisia bigelovii</i> ^b	1	12	46	4	7	0	1
<i>Artemisia cana</i>	3	43	96	13	6	0	24
<i>Artemisia longiloba</i>	1	3	8	2	1	0	0
<i>Artemisia nova</i> ^b	1	36	81	13	23	0	0
<i>Artemisia pygmaea</i> ^b	1	4	12	4	0	0	0
<i>Artemisia rigida</i> ^b	1	13	30	8	5	0	0
<i>Artemisia rothrockii</i> ^b	1	7	8	0	2	4	1
<i>Artemisia tridentata</i> ^b	5	427	1103	213	214	0	0
<i>Artemisia tripartita</i> ^b	<u>1</u>	<u>20</u>	<u>46</u>	<u>14</u>	<u>6</u>	<u>0</u>	<u>0</u>
Totals		617	1573	296	283	12	26

^a Includes only ssp. for which chromosome numbers have been determined. There are additional subspecific taxa that are cytologically unknown: *A. arbuscula* ssp. *thermopola*, *A. nova* var. *duchesnicola*, *A. tripartita* ssp. *rupicola*.

^b Some populations have plants at more than one chromosome ploidy level. The ploidy ($\times$) level reported here is that of the mode of the sampled population(s) or the lowest number when an equal number of plants were at different $\times$ levels.



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