Evolution and Taxonomy of Sagebrush

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Subgenus *Tridentatae*

Examples
Big Sagebrush, Artemisia tridentata
Six subspecies
Common: basin, mountain, Wyoming
Restricted: snowbank, xeric, Parish
<table>
<thead>
<tr>
<th>Species</th>
<th>Subspecies</th>
<th>Distribution and Site Adaptation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Low sagebrush</td>
<td>Low sagebrush</td>
<td>W. Wyoming to SC. Washington and N. California on dry sterile, rocky, shallow, alkaline, clay soils</td>
</tr>
<tr>
<td>(A. arbuscula)</td>
<td>(arbuscula)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Cleftleaf sagebrush</td>
<td>W. Wyoming, N. Utah, and E. Idaho on spring-flooded, summer-dry soils</td>
</tr>
<tr>
<td></td>
<td>(thermopola)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Lahontan low sagebrush</td>
<td>NW Nevada extending into adjacent California, Oregon and Idaho on soils of low water holding capacity and shallow depth usually around and above the old shoreline of Lake Lahontan</td>
</tr>
<tr>
<td>Coaltown sagebrush</td>
<td>(A. argillosa)</td>
<td>Jackson County, Colorado, on alkaline spoil material</td>
</tr>
<tr>
<td>Bigelow sagebrush</td>
<td>(A. bigelovii)</td>
<td>Four corners area extending to NE. Utah, SE. California, and W. Texas on rocky, sandy soils</td>
</tr>
<tr>
<td>Silver sagebrush</td>
<td>Bolander silver sagebrush</td>
<td>E. Oregon, W. Nevada, and N. California in alkaline basins</td>
</tr>
<tr>
<td>(A. cana)</td>
<td>Plains silver sagebrush</td>
<td>Generally E. of Continental Divide, Alberta and Manitoba to Colorado on loamy to sandy soils of river and stream bottoms</td>
</tr>
<tr>
<td></td>
<td>Mountain silver sagebrush</td>
<td>Generally W. of Continental Divide, Montana and Oregon to Arizona and New Mexico in mountain areas along streams and in areas of heavy snowpack</td>
</tr>
<tr>
<td>Black sagebrush</td>
<td>Black Sagebrush</td>
<td>SE. Oregon and SC. Montana to S. California and NW New Mexico on dry, shallow, stony soils with some affinity for calcareous conditions</td>
</tr>
<tr>
<td>(A. nova)</td>
<td>Duchesne black sagebrush</td>
<td>NE. Utah on reddish clay soils of Duchesne River Formation</td>
</tr>
<tr>
<td></td>
<td>(duchesnicola)</td>
<td></td>
</tr>
</tbody>
</table>
| Pygmy sagebrush  
| **(A. pygmaea)**  
| C. Nevada and NE. Utah to N. Arizona on calcareous desert soils |
| Stiff sagebrush  
| **(A. rigida)**  
| E. Oregon, WC. Idaho, and E. Washington on rocky scablands |
| Rothrock sagebrush  
| **(A. rothrockii)**  
| E. California and W. Nevada on deep soils along forest and meadow margins in Sierra Nevada and outlying mountain ranges |
| Big sagebrush  
| **(A. tridentata)**  
| Parish big sagebrush  
| **(parishii)**  
| Los Angeles basin area on deep soils in chaparral and saltbush habitats |
| Snowbank big sagebrush  
| **(spiciformis)**  
| Wyoming, Idaho, Colorado, and Utah in high mountains associated with *A. cana* ssp. *viscidula* but in slightly drier areas |
| Basin big sagebrush  
| **(tridentata)**  
| British Columbia and Montana to New Mexico and Baja California in dry, deep, well-drained soils on foothills and mountains |
| Mountain big sagebrush  
| **(vaseyana)**  
| British Columbia and Montana to S. California and N. New Mexico in deep, well-drained soils on foothills and mountains |
| Wyoming big sagebrush  
| **(wyomingensis)**  
| North Dakota and Washington to Arizona and New Mexico on shallower well-drained soils often underlain by a caliche or silica layer in valleys and on foothills |
| Xeric big sagebrush  
| **(xericensis)**  
| WC. Idaho on basaltic and granitic soils |
| Threetip sagebrush  
| **(A. tripartita)**  
| Wyoming threetip sagebrush  
| **(rupicola)**  
| W. and S. Wyoming on rocky knolls |
| Tall threetip sagebrush  
| **(tripartia)**  
| E. Washington and W. Montana to N. Nevada and N. Utah on moderate-to-deep well-drained soils |
Sagebrush Obligates* and Other Sagebrush Habitat Animals
Sage Grouse*
Brewer's Sparrow*
Sage Thrasher*
Sage Sparrow*
Pygmy Rabbit*
Sagebrush Lizard
Sagebrush Vole
Pronghorn Antelope
Mule Deer
Fig. 2. Distribution of the section (subgenus) Seriphidium in Eurasia and North Africa. The numbers indicate maximum number of species in each area.

**Tridentatae**

Subgenus limits

- Non-A. *tridensata* extension

Example of landscape domination in Utah
Table 1.—Summary of subgenus *Tridentatae* chromosome counts.

<table>
<thead>
<tr>
<th>Species</th>
<th>No. ssp.</th>
<th>No. pops.</th>
<th>No. plants</th>
<th>No. 2x</th>
<th>No. 4x</th>
<th>No. 6x</th>
<th>No. 8x</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Artemisia arbuscula</em></td>
<td>2</td>
<td>51</td>
<td>139</td>
<td>25</td>
<td>18</td>
<td>8</td>
<td>0</td>
</tr>
<tr>
<td><em>Artemisia argillosa</em></td>
<td>1</td>
<td>1</td>
<td>4</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Artemisia bigelovii</em></td>
<td>1</td>
<td>12</td>
<td>46</td>
<td>4</td>
<td>7</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td><em>Artemisia cana</em></td>
<td>3</td>
<td>43</td>
<td>96</td>
<td>13</td>
<td>6</td>
<td>0</td>
<td>24</td>
</tr>
<tr>
<td><em>Artemisia longiloba</em></td>
<td>1</td>
<td>1</td>
<td>8</td>
<td>2</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Artemisia nova</em></td>
<td>1</td>
<td>36</td>
<td>81</td>
<td>13</td>
<td>23</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Artemisia pygmaea</em></td>
<td>1</td>
<td>1</td>
<td>12</td>
<td>4</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Artemisia rigida</em></td>
<td>1</td>
<td>13</td>
<td>30</td>
<td>8</td>
<td>5</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Artemisia rothrockii</em></td>
<td>1</td>
<td>1</td>
<td>8</td>
<td>0</td>
<td>2</td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td><em>Artemisia tridentata</em></td>
<td>5</td>
<td>427</td>
<td>1,103</td>
<td>213</td>
<td>214</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Artemisia tripartita</em></td>
<td>1</td>
<td>2</td>
<td>46</td>
<td>14</td>
<td>6</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><strong>Totals</strong></td>
<td>617</td>
<td>1,573</td>
<td>296</td>
<td>283</td>
<td>12</td>
<td>26</td>
<td></td>
</tr>
</tbody>
</table>
Molecular and Morphological Differentiation in *Artemisia*

Disk Flowers

Two Disk Flowers And One Ray Flower

Two Disk Flowers And One Ray Flower

cp DNA
COUMARINS
Artemisia tridentata ssp. wyomingensis
Similarity of Individuals and Populations
Fig. 1. Fluorochrome banding with chromomycin (a, c, e, f, g, i, k), fluorescent in situ hybridization (b, d, h, j, l) and haploid idiograms (m-r) of the different taxa studied. Scale bars = 10 μm for photographs and idiograms. (a, b, m) A. argillosa. (c, d, n) A. cana ssp. bolanderi. (c, f, o) A. filifolia. (g, h, p) A. pygmaea. (i, j, q) A. rigida; arrows in picture "i" indicate B chromosomes. (k, l, r) A. tripartita ssp. rupicola. Chromomycin ■ DAPI ■ 18S-5.8S-26S rDNA loci ■ 5S rDNA loci
<table>
<thead>
<tr>
<th>Taxon</th>
<th>2n</th>
<th>Ploidy level</th>
<th>Chromosomal formula</th>
<th>MCL (SD) (μm)</th>
<th>CLR (μm)</th>
<th>TKL (SD) (μm)</th>
<th>CI</th>
<th>R</th>
<th>A1</th>
<th>A2</th>
<th>Stebbins Class</th>
<th>2C (pg)</th>
<th>NORs</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. argillosa</td>
<td>36</td>
<td>4x</td>
<td>30 m + 6 sm</td>
<td>6.11 (1.08)</td>
<td>2.76 – 8.36</td>
<td>226.76 (9.00)</td>
<td>43.07</td>
<td>1.16</td>
<td>0.24</td>
<td>0.17</td>
<td>1B</td>
<td>15.77</td>
<td>8(4)</td>
</tr>
<tr>
<td>A. cano ssp bolanderi</td>
<td>18</td>
<td>2x</td>
<td>14 m + 4 sm</td>
<td>6.17 (0.77)</td>
<td>5.09 – 7.32</td>
<td>111.14 (2.50)</td>
<td>42.63</td>
<td>1.76</td>
<td>0.25</td>
<td>0.13</td>
<td>2A</td>
<td>9.01</td>
<td>6(1)</td>
</tr>
<tr>
<td>A. filifolia</td>
<td>18 + (0–2)B</td>
<td>2x</td>
<td>14 m + 2 m&lt;sub&gt;sat&lt;/sub&gt; + sm + sm&lt;sub&gt;sat&lt;/sub&gt;</td>
<td>4.76 (0.61)</td>
<td>3.88 – 5.58</td>
<td>85.75 (1.35)</td>
<td>44.97</td>
<td>1.22</td>
<td>0.18</td>
<td>0.13</td>
<td>1A</td>
<td>7.26</td>
<td>4(1)</td>
</tr>
<tr>
<td>A. pygmaea</td>
<td>18 + (0–1)B</td>
<td>2x</td>
<td>12 m + 2 m&lt;sub&gt;sat&lt;/sub&gt; + 2 sm + 2 sm&lt;sub&gt;sat&lt;/sub&gt;</td>
<td>7.08 (0.56)</td>
<td>6.13 – 8.04</td>
<td>127.53 (3.43)</td>
<td>44.43</td>
<td>1.70</td>
<td>0.19</td>
<td>0.08</td>
<td>1A</td>
<td>11.14</td>
<td>6(3)</td>
</tr>
<tr>
<td>A. rigida</td>
<td>18 + (0–4)B</td>
<td>2x</td>
<td>14 m + 2 m&lt;sub&gt;sat&lt;/sub&gt; + sm + sm&lt;sub&gt;sat&lt;/sub&gt;</td>
<td>5.57 (0.49)</td>
<td>4.95 – 6.34</td>
<td>100.25 (5.75)</td>
<td>44.29</td>
<td>1.13</td>
<td>0.19</td>
<td>0.09</td>
<td>2A</td>
<td>8.23</td>
<td>6(3)</td>
</tr>
<tr>
<td>A. tripartita ssp. rupicola</td>
<td>18</td>
<td>2x</td>
<td>14 m + 4 sm</td>
<td>5.75 (0.53)</td>
<td>4.96 – 6.40</td>
<td>103.61 (3.11)</td>
<td>42.31</td>
<td>1.18</td>
<td>0.26</td>
<td>0.09</td>
<td>1A</td>
<td>8.68</td>
<td>6(3)</td>
</tr>
</tbody>
</table>

The superscripts indicate: 1 chromosomal formula according to Levan et al. (1964); 2 mean chromosome length; 3 chromosome length range; 4 total karyotype length; 5 centromeric index (I index in Levan et al. 1964); 6 length ratio of long and short chromosome arms (Levan et al. 1964); 7 intrachromosomal asymmetry index (Romero 1986); 8 interchromosomal asymmetry index (Romero 1986); 9 symmetry class according to Stebbins (1971); 10 2C nuclear DNA content in pg (Garcia et al., unpubl. data); 11 Number of NORs detected with silver staining (the most frequent number is given, followed by the maximum number observed in brackets).
Artemisia tridentata ssp. parishii

Upright phenotype

Droopy phenotype
Hybridization & Hybrid Zones

• Mayr (1963): The evolutionary importance of hybridization seems small in the better-known groups of animals.
• Harrison (1993): Despite the supposed rarity of animal hybrids in nature, hybridization has been a major focus of studies in animal evolution.
• Stebbins (1959): Hybridization between distinct forms (species or subspecies) is the rule in flowering plants.
• Harrison (1993): Plant hybrid zones tend to be diffuse (not geographically well defined) and are often characterized by local hybrid swarms. In many instances, hybridization appears to occur at ecotones or boundaries between different habitats.
Hybrid Zone Theory
Hypotheses

Dynamic Equilibrium Hybrid Zone Model
(Barton & Hewitt 1985)
Hybrids Inferior
Independent of Environment
Stabilization Achieved by Hybrid Inferiority and
Gene Flow Across Zone

Mosaic Hybrid Zone Model (Harrison & Rand 1986)
Hybrids Inferior
Parentals in Habitat Mosaics

Bounded Hybrid Superiority Hybrid Zone Model
(Moore 1977)
Hybrids Superior (Only in Hybrid Zone)
SALT CREEK CANYON
HYBRID ZONE

Mountain Zone, Endophyte M
1880-1920 m, ASL

Hybrid Zone, Endophyte Hy
1840-1870 m, ASL

Basin Zone, Endophyte Ba
1790-1830 m, ASL
Reciprocal Transplants and Soil Transfer Experiments
Salt Cave Hollow Reciprocal Transplant Gardens

Basin Garden

Mountain Garden

Middle Hybrid Garden
Summary of Sagebrush Hybrid Zone Studies

- Plant morphology
- Selection and hybrid fitness
- Developmental instability
- Reciprocal transplants
- Community biology
- Soil properties and soil translocation
- Respiration and water potential
- Spatial distribution of terpenes
- Soil microflora
- Insects and galls (+ common garden)
- Soil microflora and root endophytes
- Genetic Markers
Sagebrush hybrid zone, a hitch-hiker’s guide to speciation

Double reciprocal transplant experiments of plants (parentals and hybrids) and soils across the big sagebrush hybrid zone showed that fungal endophytes interact with the soils and different plant genotypes conferring enhanced plant reproduction in the soil native to the endophyte and reduced reproduction in soils alien to the endophyte. One endophyte enhanced only hybrid reproduction. Because endophytes are passed to the next generation of plants on seed coats, this interaction confers a selective advantage, habitat specificity, and the means of restricting gene flow making the hybrid zone stable and narrow; potentially leading to speciation.
Evolutionary Consequences of Stable Hybrid Zones in Subgenus *Tridentatae*

- Reservoir of fit hybrid plants.
- Source for differentiation of new genetic combinations.
- Exploit new habitats as environmental conditions change.
- Formula for success for land dominance.
SAGEBRUSH GENETICS AND HYBRIDIZATION SUMMARY

• MONOPHYLETIC GROUP
• HYBRIDIZATION IMPORTANT
• POLYPLOIDY PLAYS A SIGNIFICANT ROLE
• MOLECULAR GENETICS IS BECOMING IMPORTANT TOOL
Seeding Big Sagebrush

Requires:

Firm Seedbed, Little Soil Coverage

Successful Research Techniques:

Broadcast and Covering

Seeding on Snow

Seed Dribbler

Brillion, Jarbridge Sagebrush Seeder

However,

Operational Scale Seedings Often Fail
Establishment of Aerially Seeded Wyoming Big Sagebrush Following Southern Idaho Wildfires

Boise State University (Lynse and Wicklow-Howard), RMRS (Shaw), and BLM (Pellant and Eldridge) Cooperating

• Examined 35 Wyoming big sagebrush seeding (1987-2000) and adjacent non-seeded areas
• No big sagebrush on 23 seeded areas; native recruitment on one-fourth of non-seeded areas
• Big sagebrush densities were similar on seeded and control areas
• Densities on seeded plots averaged 90-500 plants/ha
• Seeding rates ranged from 220,000 to 2.7 million seeds/ha
Establishment of Aerially Seeded Wyoming Big Sagebrush Following Wildfires in Southern Idaho

- Sagebrush subspecies on the 12 seeded areas with big sagebrush
  - 4 with only Wyoming big sagebrush
  - 4 with Wyoming big sagebrush and other subspecies
  - 4 with only mountain and basin big sagebrush
Seeded Bluebunch Wheatgrass and Wyoming Big Sagebrush, West of Elko, Nevada
The geographic distribution of each species serves as the geographic boundary for the 11 seed zones, with the additional restriction that seed should not be moved farther than 483 km (300 miles) to its target planting site, and if less than 483 km, not outside of its native distribution. Except for *A. tridentata*, no additional transfer guidelines are proposed for changes in elevation within a seed zone. When local data suggest moisture gradients and ranges of elevation in excess of 458 m (1,500 feet), conservative guidelines could further restrict seed transfer up 153 m (500 feet) in elevation, or down 305 m (1000 feet) in elevation, from the origin collection area. Correctly applied, seed and plant transfer guidelines minimize the risk of planting maladapted stock, increasing the survival and reproductive success to achieve restoration, rehabilitation, reclamation, and wildlife habitat improvement objectives.
SAGEBRUSH SEED TRANSFER GUIDELINES

• In determining species mix, it is more important to match a species to its native environment, rather than choosing a subspecies of big sagebrush for wildlife or livestock preferred forage.

• Hybrid zones have allowed A. tridentata to be widely adaptable. Hybrid zones are suitable for seed collection for restoration, i.e., don’t have to avoid hybrid zones for gene conservation diversity concerns, as hybridization contributes to the versatility of big sagebrush.

• Do not move seed from a collection site farther than 300 miles to its target planting site, and if less than 300 miles, not outside of its native distribution.

• Upland Wyoming big sagebrush is more drought hardy than floodplain basin big sagebrush. Basin big sagebrush is a prolific seed producer and its seed is readily available, but planting basin big sagebrush on uplands sites is risky.
Sagebrush Management Issues

• Habitat values are generally recognized
• Some concern about closed, decadent stands (but more concern fragmented and lost stands)—see Peterson (1995) and Welch (2005)
• Some recent studies:
  – McAdoo et al. (2004), Summers (2005); Mechanical treatment to renew stands; value of mosaics
  – Northeastern Wyoming
    • Schuman and Belden (2002), Partlow et al. (2004); Vickland et al. (2004); sagebrush and grass seeding rates and wildlife use
    • Booth et al. (2003, 2004); Fencing
    • Olson et al. (2000), Booth (2002), mixed shrub seedings with fourwing saltbush
    • Stahl et al. (1998), mycorrhizae
• Sage-Grouse Habitat Restoration Symposium Proceedings (RMRS-P-38, Shaw, Pellant, and Monsen 2005):
  • Roundy; Plant success and approaches to community restoration
  • Walker and Shaw; Current and Potential use of broadleaf herbs…
  • Lambert; Seeding considerations in restoring big sagebrush habitat
  • Lynse; Restoring Wyoming big sagebrush
  • Shaw et al.; Reseeding big sagebrush: techniques and issues
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