Evolution and Taxonomy of Sagebrush

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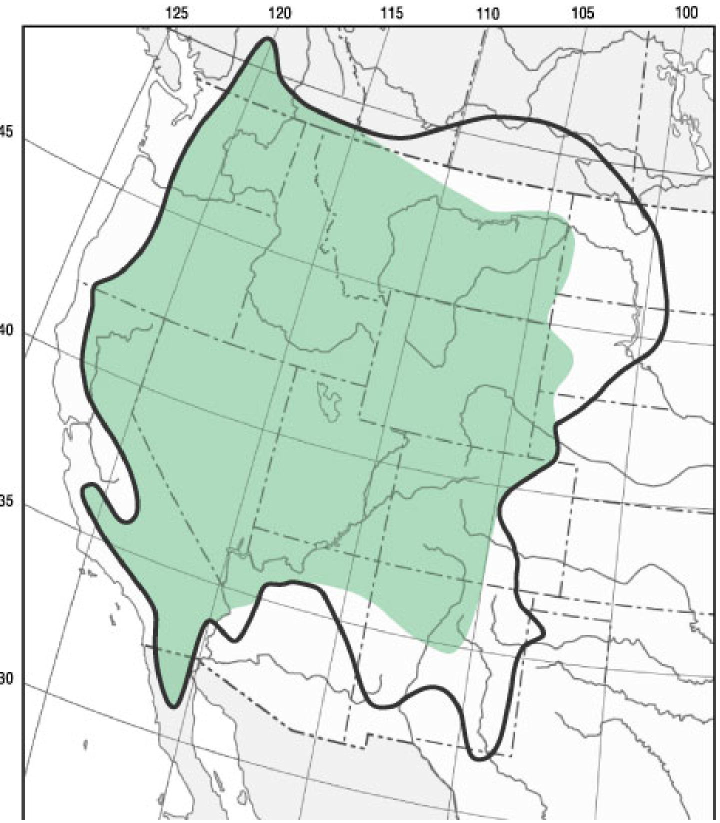
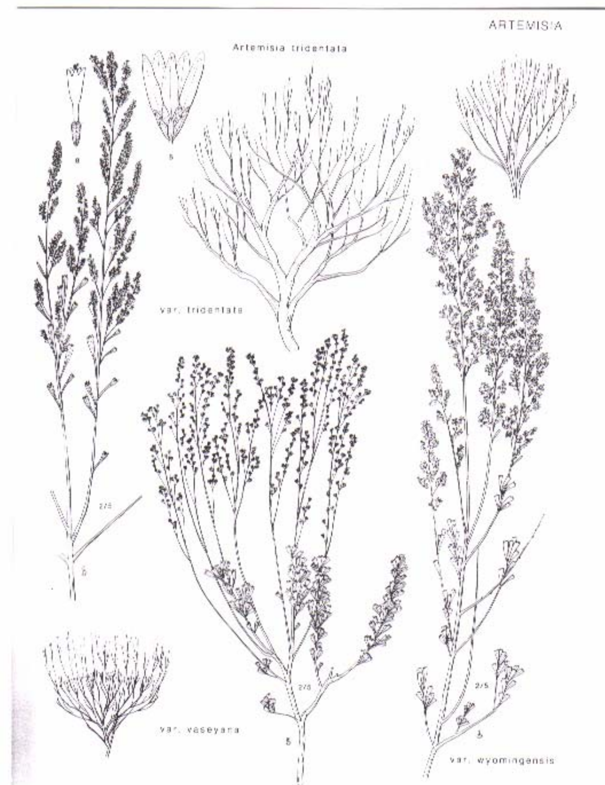
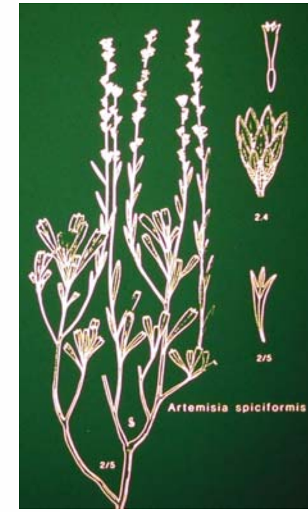
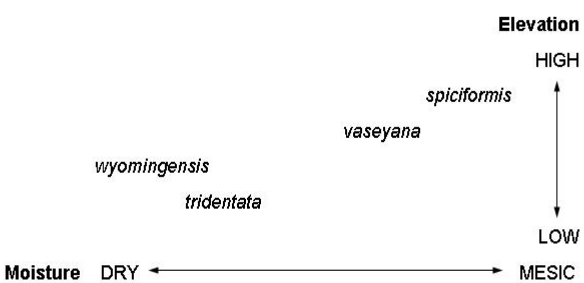
Subgenus *Tridentatae* Examples

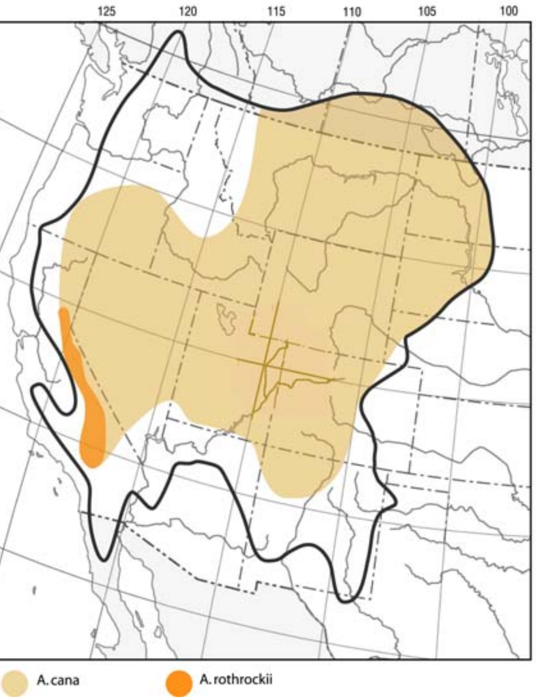


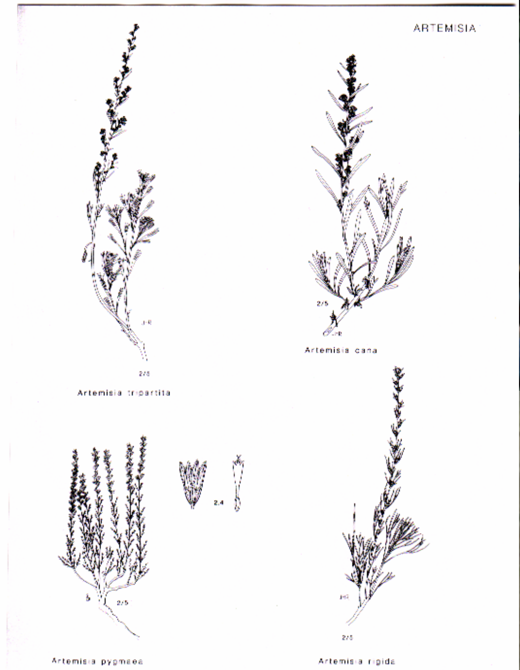


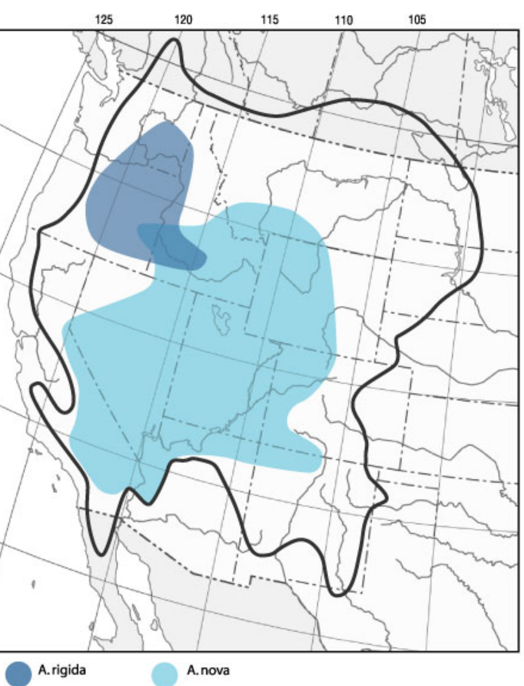


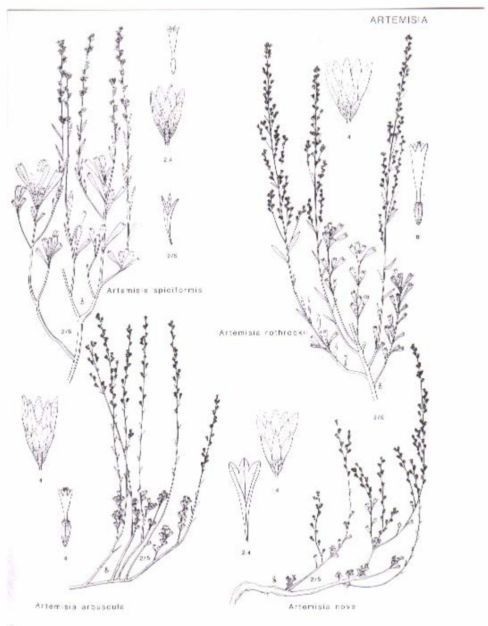


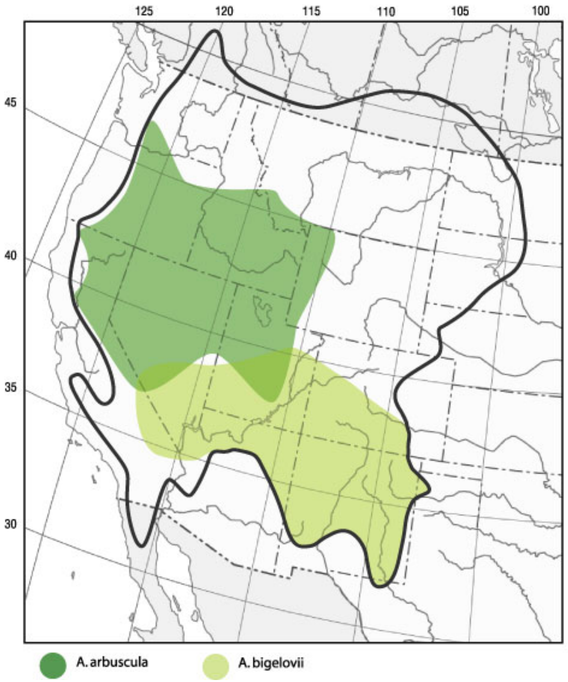
Big Sagebrush, *Artemisia tridentata*
Six subspecies
Common: basin, mountain, Wyoming
Restricted: snowbank, xeric, Parish

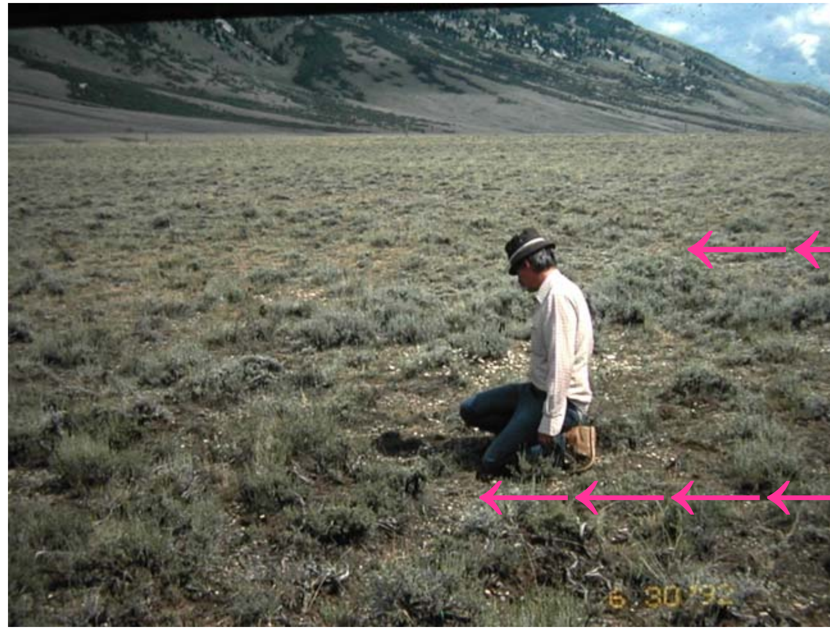

125
120
115
110
105
100
A. cana
A. rothrockii


ARTEMISIA
Artemisia tripartita
Artemisia cana
Artemisia pygmaea
Artemisia rigida


125
120
115
110
105
A. rigida
A. nova

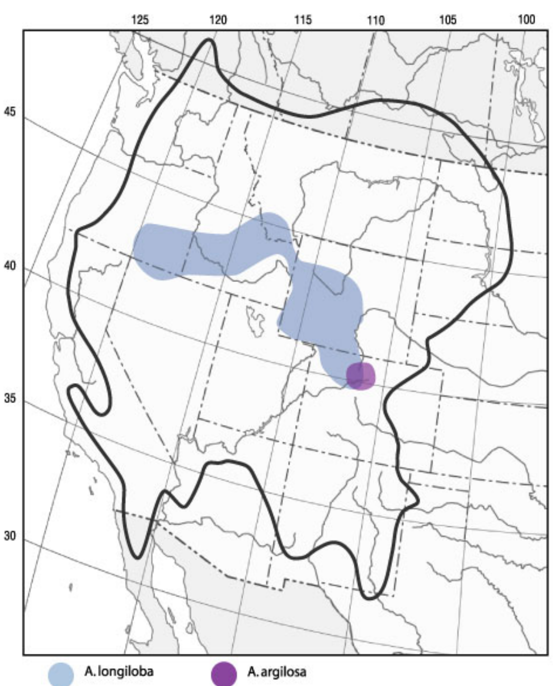

ARTEMISIA
Artemisia spiciformis
Artemisia rothrockii
Artemisia arbuscula
Artemisia nova



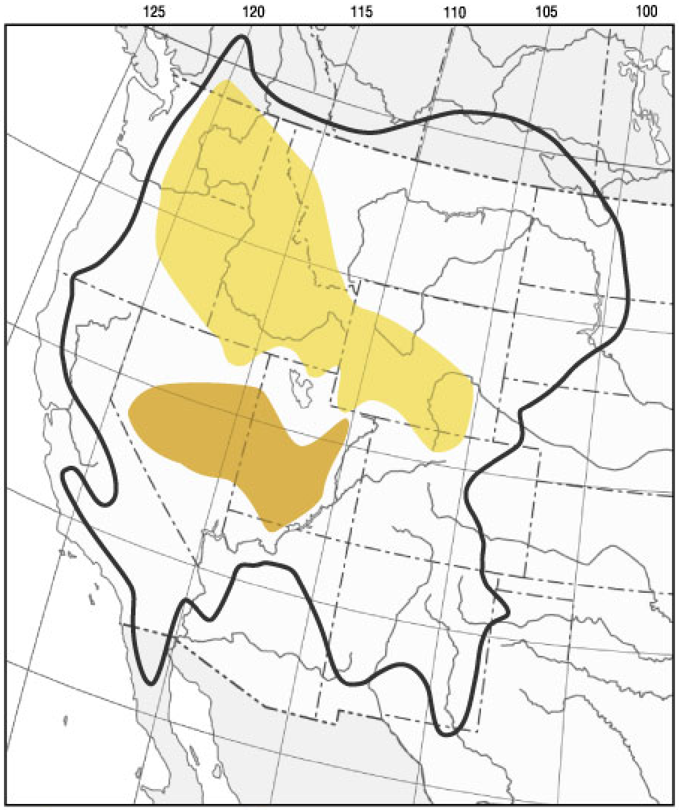


Artemisia arbuscula

Artemisia nova



Artemisia logiloba



A. tripartita A. pygmaea

Species	Subspecies	Distribution and Site Adaptation
Low sagebrush (*A. arbuscula*)	Low sagebrush *(arbuscula)*	W. Wyoming to SC. Washington and N. California on dry sterile, rocky, shallow, alkaline, clay soils
	Cleftleaf sagebrush (*thermopola*)	W. Wyoming, N. Utah, and E. Idaho on spring-flooded, summer-dry soils
	Lahontan low sagebrush	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
Coaltown sagebrush (*A. argillosa*)		Jackson County, Colorado, on alkaline spoil material
Bigelow sagebrush (*A. bigelovii*)		Four corners area extending to NE. Utah, SE. California, and W. Texas on rocky, sandy soils
Silver sagebrush (*A. cana*)	Bolander silver sagebrush	E. Oregon, W. Nevada, and N. California in alkaline basins
	Plains silver sagebrush	Generally E. of Continental Divide, Alberta and Manitoba to Colorado on loamy to sandy soils of river and stream bottoms
	Mountain silver sagebrush	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 (*A. longiloba*)		SW. Montana, NW. 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 (*A. nova*)	Black Sagebrush	SE. Oregon and SC. Montana to S. California and NW New Mexico on dry, shallow, stony soils with some affinity for calcareous conditions
	Duchesne black sagebrush (*duchesnicola*)	NE. Utah on reddish clay soils of Duchesne River Formation

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

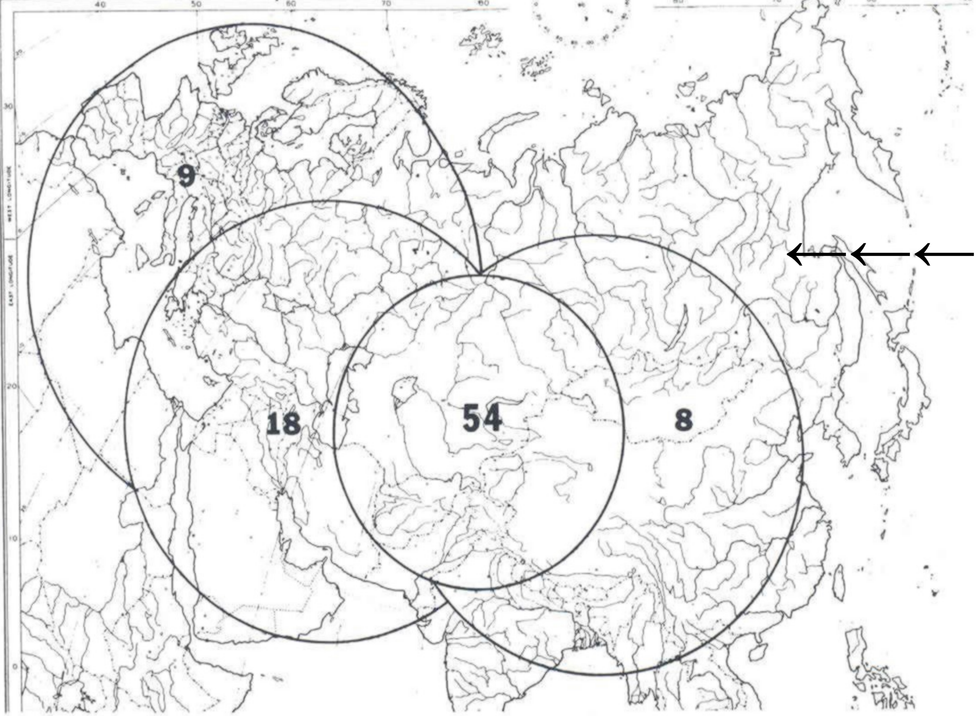
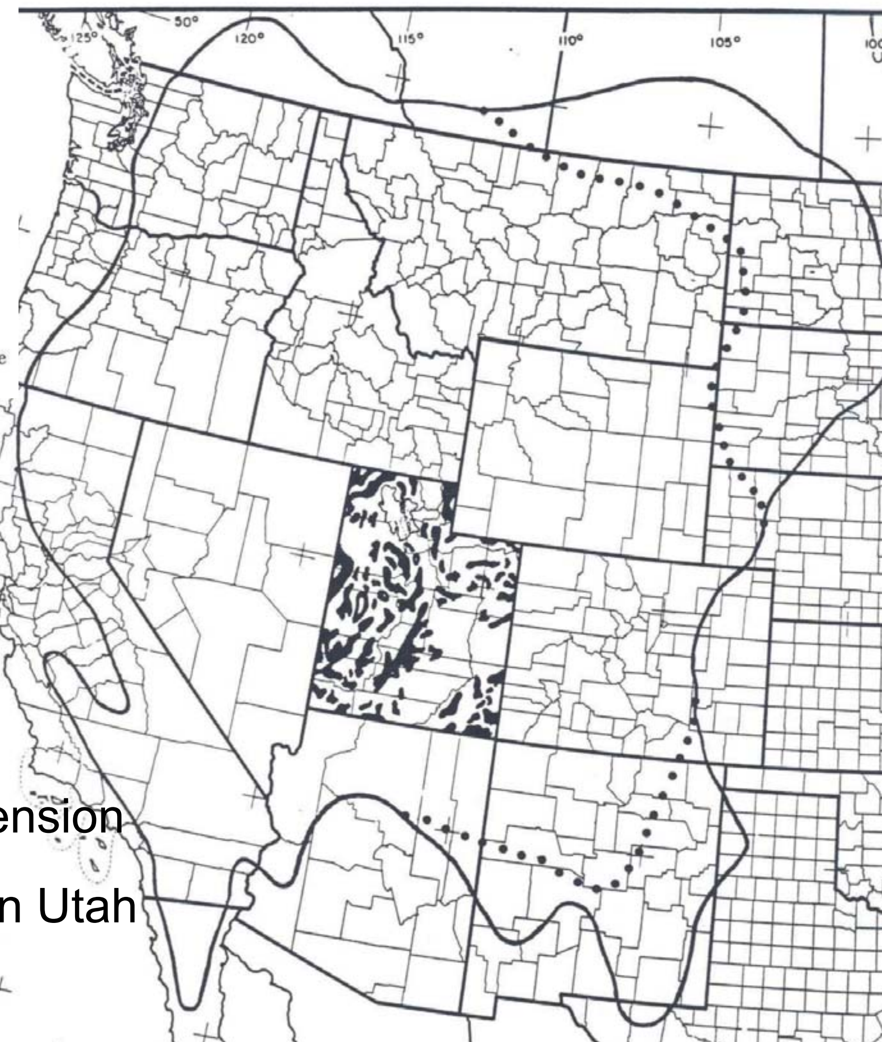


Fig. 2. Distribution of the section (subgenus) Seriphidium in Eurasia and North Africa. The numbers indicate maximum number of species in each area.

←←←*Seriphidium*



Tridentatae→→→

Subgenus limits

Non-*A. tridendata* extension

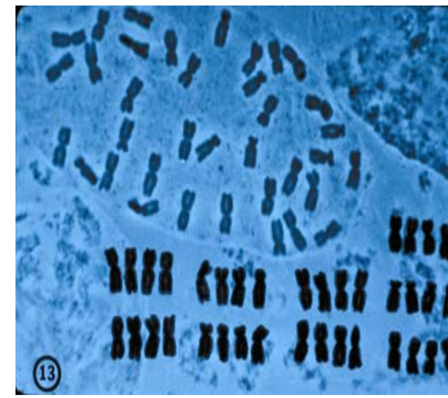
Example of landscape domination in Utah

CYTOGENETICS

McArthur and Sanderson 42

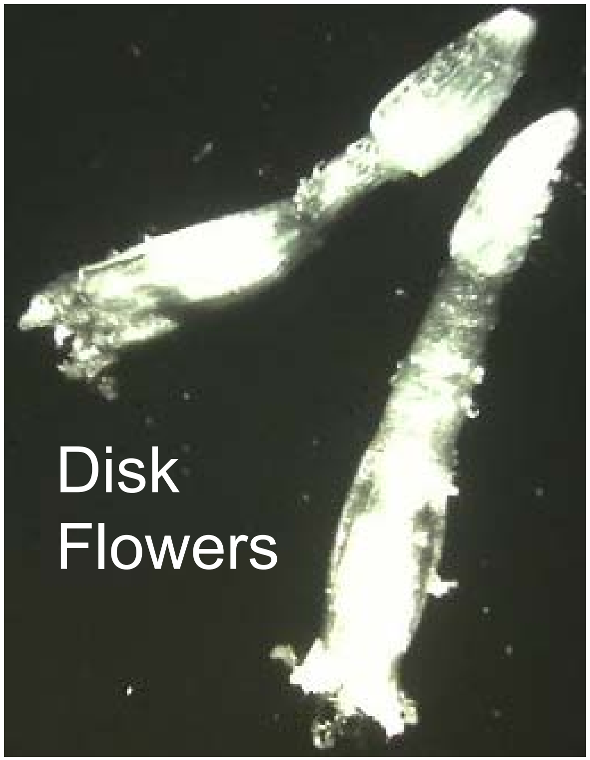
Table 1.--Summary of subgenus Tridentatae chromosome counts.[a]

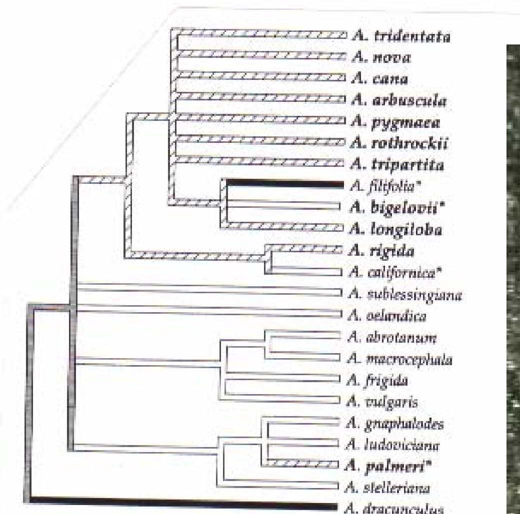
Species	No. ssp.[b]	No. pops.	No. plants	No. pops.[c] at 2x	4x	6x	8x
Artemisia arbuscula[c,d]	2	51	139	25	18	8	0
Artemisia argillosa	1	1	4	0	1	0	0
Artemisia bigelovii[c]	1	12	46	4	7	0	1
Artemisia cana	3	43	96	13	6	0	24
Artemisia longiloba	1	3	8	2	1	0	0
Artemisia nova[c]	1	36	81	13	23	0	0
Artemisia pygmaea[c]	1	4	12	4	0	0	0
Artemisia rigida[c]	1	13	30	8	5	0	0
Artemisia rothrockii[e]	1	7	8	0	2	4	1
Artemisia tridentata[c,d]	5	427	1,103	213	214	0	0
Artemisia tripartita[c]	1	20	46	14	6	0	0
Totals		617	1,573	296	283	12	26



Karyotype of 4X Autotetraploid *Artemisia rigida*

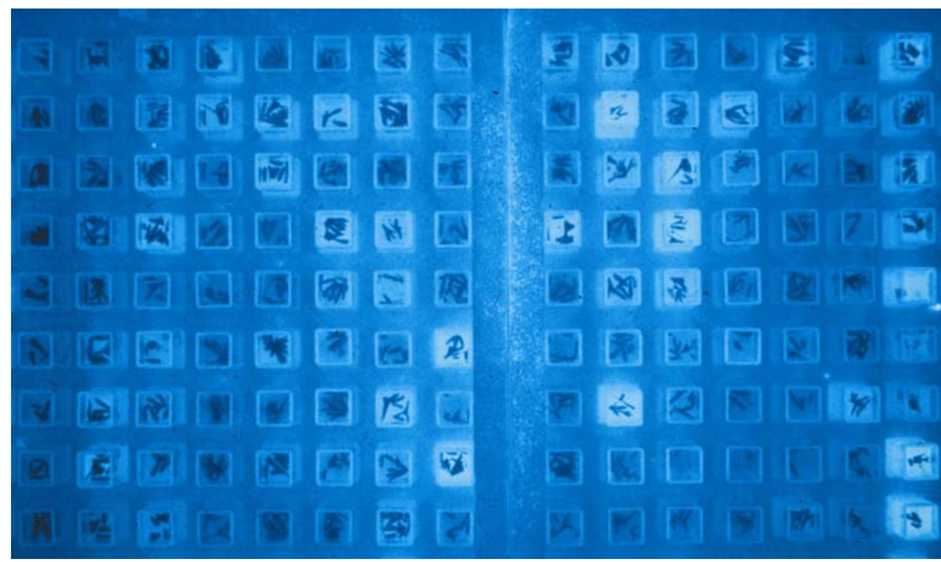
Molecular and Morphological Differentiation in *Artemisia*

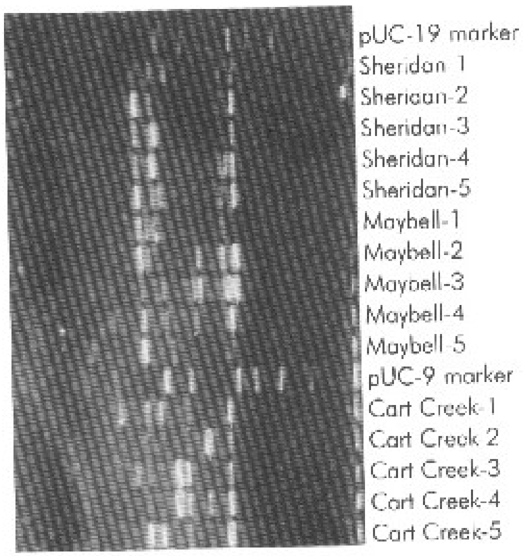




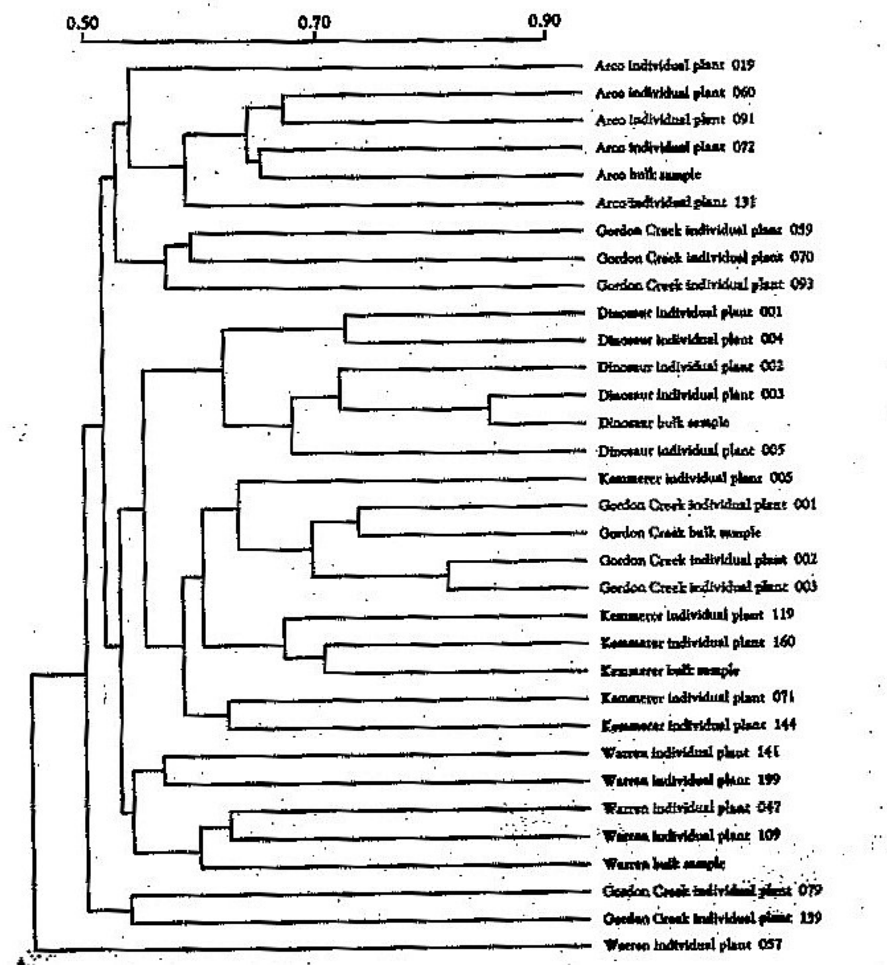
cp DNA

COUMARINS





Artemisia RAPDs



Artemisia tridentata ssp. *wyominginsis*
Similarity of Individuals and Populations

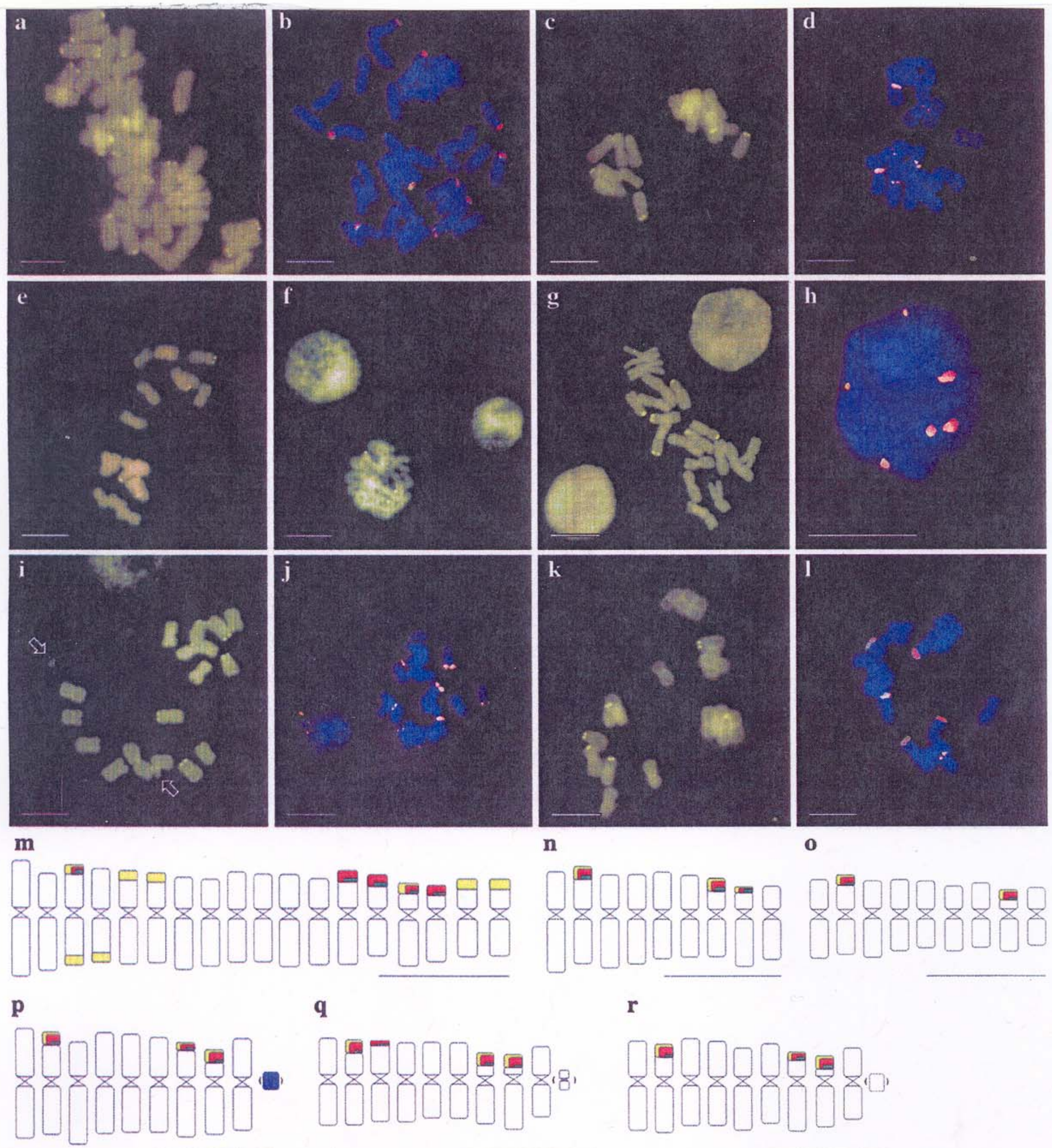
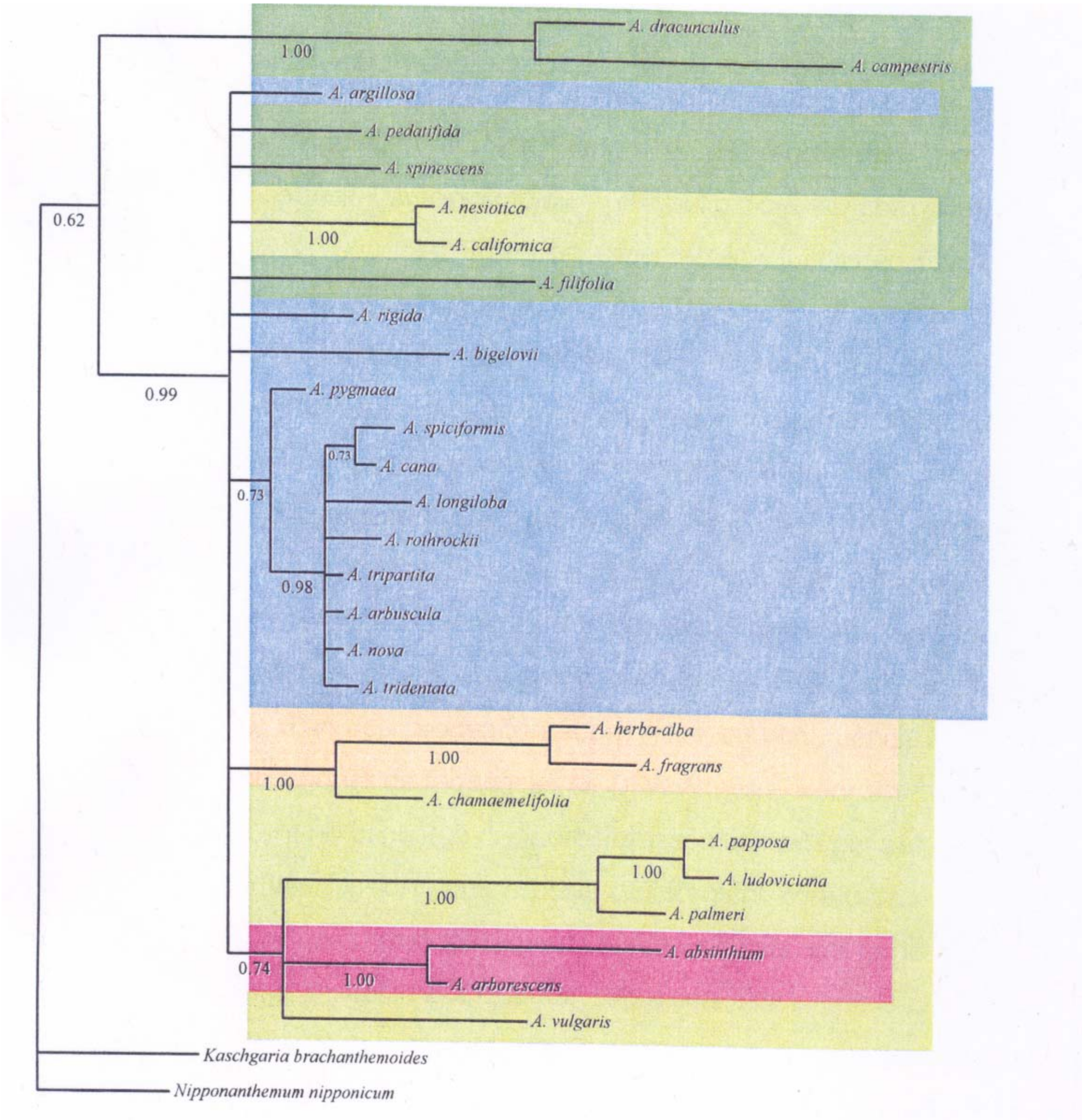


Fig. 1. Fluorochrome banding with chromomycin (**a**, **c**, **e**, **f**, **g**, **i**, **k**), fluorescent *in situ* hybridization (**b**, **d**, **h**, **j**, **l**) and haploid idiograms (**m-r**) of the different taxa studied. Scale bars = 10 μm for photographs and idiograms. (a, b, m) *A. argillosa*. (c, d, n) *A. cana* ssp. *bolanderi*. (e, 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 2. Karyological data

Taxon	2*n*	Ploidy level	Chromosomal formula[1]	MCL[2] (SD) (μm)	CLR[3] (μm)	TKL[4] (SD) (μm)	CI[5]	R[6]	A1[7]	A2[8]	Stebbins Class[9]	2C [10] (pg)	NORs[11]
A. argillosa	36	4*x*	30 m + 6 sm	6.11 (1.08)	2.76 – 8.36	226.76 (9.00)	43.07	1.16	0.24	0.17	1B	15.77	8(4)
A. cana ssp. *bolanderi*	18	2*x*	14 m + 4 sm	6.17 (0.77)	5.09 – 7.32	111.14 (2.50)	42.63	1.76	0.25	0.13	2A	9.01	6(1)
A. filifolia	18 + (0–2)B	2*x*	14 m + 2 m^{sat} +sm + sm^{sat}	4.76 (0.61)	3.88 – 5.58	85.75 (1.35)	44.97	1.22	0.18	0.13	1A	7.26	4(1)
A. pygmaea	18 + (0–1)B	2*x*	12 m + 2 m^{sat} +2 sm + 2 sm^{sat}	7.08 (0.56)	6.13 – 8.04	127.53 (3.43)	44.43	1.70	0.19	0.08	1A	11.14	6(3)
A. rigida	18 + (0–4)B	2*x*	14 m + 2 m^{sat} +sm + sm^{sat}	5.57 (0.49)	4.95 – 6.34	100.25 (5.75)	44.29	1.13	0.19	0.09	2A	8.23	6(3)
A. tripartita ssp. *rupicola*	18	2*x*	14 m + 4 sm	5.75 (053)	4.96 – 6.40	103.61 (3.11)	42.31	1.18	0.26	0.09	1A	8.68	6(3)

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)


A. dracunculus
1.00
A. campestris
A. argillosa
A. pedatifida
A. spinescens
0.62
A. nesiotica
1.00
A. californica
A. filifolia
A. rigida
A. bigelovii
0.99
A. pygmaea
A. spiciformis
0.73
A. cana
0.73
A. longiloba
A. rothrockii
A. tripartita
0.98
A. arbuscula
A. nova
A. tridentata
A. herba-alba
1.00
A. fragrans
1.00
A. chamaemelifolia
A. papposa
1.00
A. ludoviciana
1.00
A. palmeri
A. absinthium
0.74
1.00
A. arborescens
A. vulgaris
Kaschgaria brachanthemoides
Nipponanthemum nipponicum


Artemisia tridentata ssp. parishii
6401
Upright phenotype
Droopy phenotype

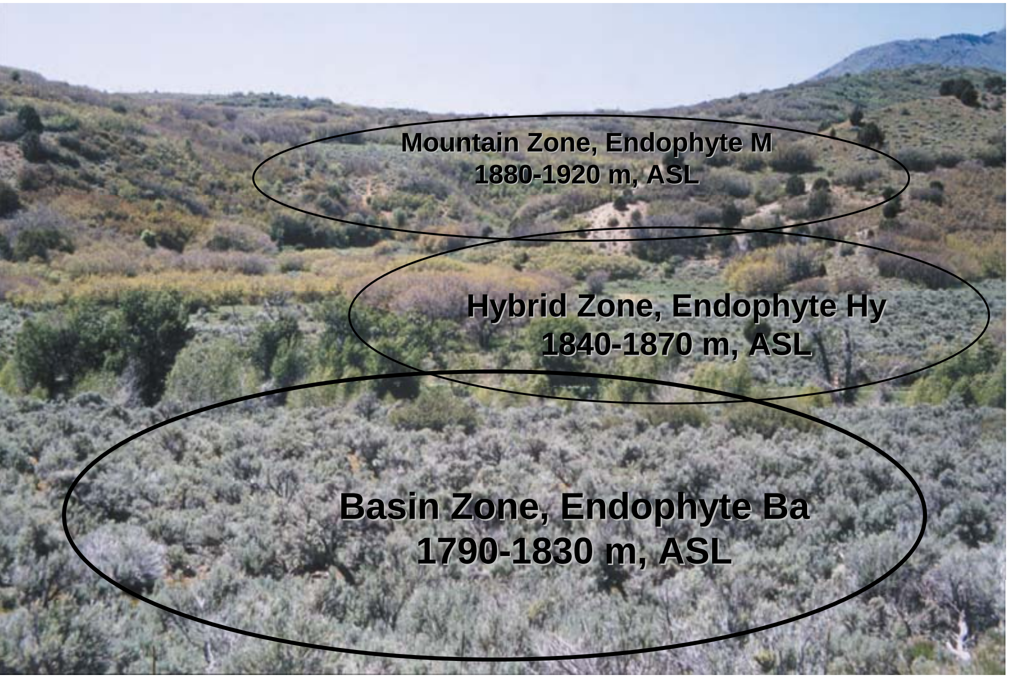
Hybridization & Hybrid Zones

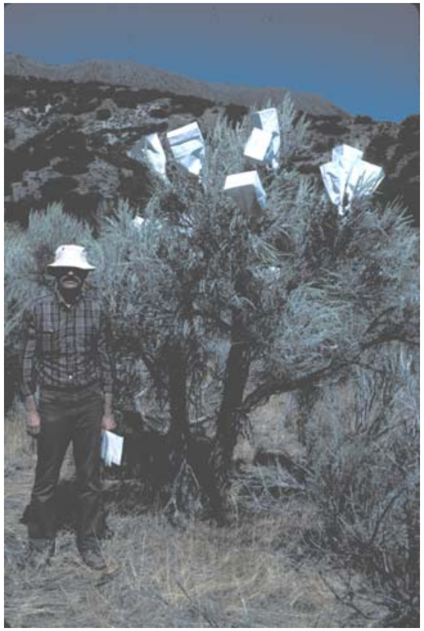
- Mayr (1963): The evolutionary importance of hybridization seems small in the better-known groups of animals.
- Harrison (1993): Despite the supposed rarity of animal hybrids in nature, hybridization has been a major focus of studies in animal evolution.
- Stebbins (1959): Hybridization between distinct 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 boundries between different habitats.

Hybrid Zone Theory Hypotheses

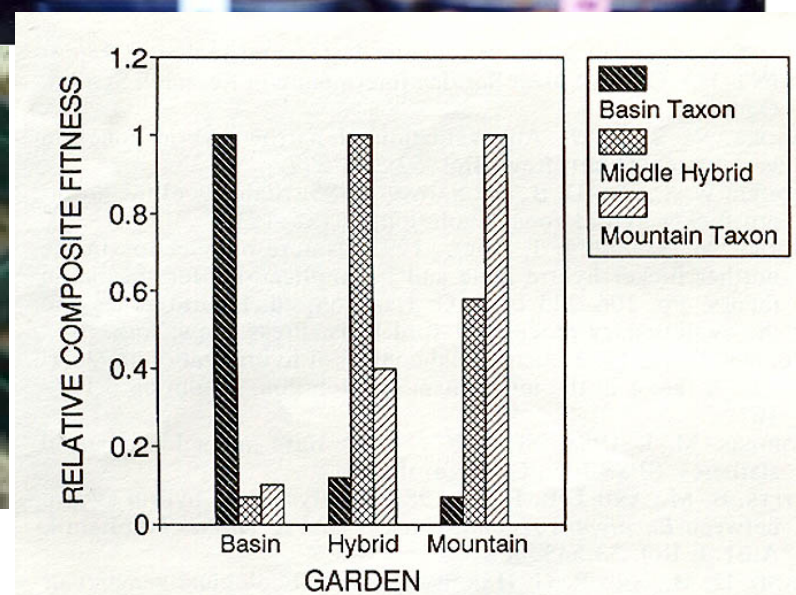
- Dynamic Equilibrium Hybrid Zone Model (Barton & Hewitt 1985)
  - Hybrids Inferior
  - Independent of Environment
  - Stabilization Achieved by Hybrid Inferiority and Gene Flow Across Zone
- Mosaic Hybrid Zone Model (Harrison & Rand 1986)
  - Hybrids Inferior
  - Parentals in Habitat Mosaics
- Bounded Hybrid Superiority Hybrid Zone Model (Moore 1977)
  - Hybrids Superior (Only in Hybrid Zone)

SALT CREEK CANYON HYBRID ZONE





Reciprocal Transplants and Soil Transfer Experiments



Salt Cave Hollow Reciprocal Transplant Gardens

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

<u>Requires:</u>

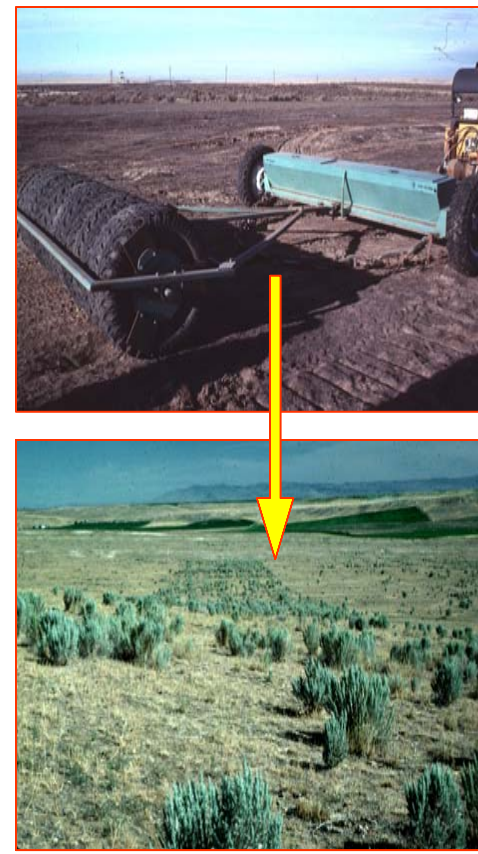
Firm Seedbed, Little Soil Coverage

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

Sagebrush (*Artemisia* spp.) Seed and Plant Transfer Guidelines

Mahalovich and McArthur, Native Plant Journal 5: 141-147 (2004)

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 succession 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

Acknowledgements

Rocky Mountain Research Station

National Fire Plan

Great Basin Native Plant Selection and Increase Project

USDA CSREES

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- **Carl Freeman, Han Wang, and Kathy Miglia, Wayne State University**
- **Joan Vallès and Sonia Garcia, University of Barcelona**