USDA Forest Service
Research Paper INT-141
1973

CHROMATOGRAPHIC CHARACTERISTICS AND PHYLOGENETIC RELATIONSHIPS OF *ARTEMISIA*, SECTION *TRIDENTATAE*

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E. Durant McArthur, Richard Stevens,
and A. Perry Plummer

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Ogden, Utah 84401

CORRIGENDUM

Artemisia bigelovii has been inadvertently and consistently misspelled throughout this publication as *Artemisia biglovii*. Correct spelling is *Artemisia bigelovii*.

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Federal aid in wildlife restoration funds
was provided through Project W-82-R

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ACKNOWLEDGMENT

We thank R. Drobnick and R. B. Ferguson, and Drs. R. G. Krebill, E. Schlatterer, H. C. Stutz, and R. K. Vickery, Jr., for critically reviewing an earlier draft of this paper. This work was facilitated by use of study plots on land belonging to the Utah Division of Wildlife Resources and the Snow Field Station of the Utah Agricultural Experiment Station and of Snow College. Some plant material was collected and/or identified by A. C. Blauer, B. C. Giunta, K. R. Jorgensen, A. McLean, and G. A. Van Epps.

CONTENTS

ABSTRACT

On the basis of a chromatographic analysis, Artemisia tridentata is divided into seven subgroups: three of subspecies vaseyana, three of subspecies tridentata, and one of subspecies wyomingensis. The three subgroups included in A. tridentata subsp. tridentata show low utilization by game and livestock; the four subgroups included in subspecies vaseyana and wyomingensis show high utilization, especially on winter ranges. Although each subgroup occupies a distinctive ecological habitat, few consistent morphological differences are manifested, particularly among the subgroups of subspecies vaseyana and subspecies tridentata.

Chromatographic comparison of the species in the section Tridentatae suggests that subgroup IIc of A. tridentata subsp. tridentata may have been the ancestral form to develop from A. biglovii. In turn, this form probably gave rise to the remaining subgroups of A. tridentata and most other species in this section.

INTRODUCTION

Sagebrush species of the genus *Artemisia* section *Tridentatae*[1] occur discontinuously as dominants or partial dominants on over one-third of that portion of the contiguous United States west of 102° W. longitude (Beetle 1960). Some of these taxa also occur in adjacent areas to the east and in Canada and Mexico. Sagebrush is an important constituent on much of the West's rangeland. It serves as forage for wildlife and livestock and as cover for birds and small animals. Moreover, sagebrush has watershed and recreation values.

Section *Tridentatae* is noted for both intraspecific and interspecific morphological variation (Hall and Clements 1923; Ward 1953; Beetle 1960, 1970). Hybridization and, to a lesser extent, introgression contribute to the morphological plasticity of the *Tridentatae*. These processes have been important in the reticulate evolutionary past of the section. Despite the variability of the group, Beetle's (Beetle 1960; Beetle and Young 1965) taxonomic treatment approaches practical workability.

Cytological studies were initiated by Diettert (1938). Diettert's and subsequent studies show the *Tridentatae* to be a polyploid series based on the chromosome number of x = 9 (Clausen and others 1940; Ward 1953; Taylor and others 1964; Winward 1970). Diploid (n = 9), tetraploid (n = 18), hexaploid (n = 27), and octoploid (n = 36) populations have been discovered. Although chromosome numbers for over 50 populations have been determined, no detailed meiotic or karyotypic studies have been performed. The chromosome numbers now available do not clarify the phylogenetic relationships within the *Tridentatae* over most of its range. However, in areas of the Northwest, diploid and tetraploid populations appear to be clearly separated by elevation (Ward 1953; Taylor and others 1964).

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[1]In this paper, section *Tridentatae* Rydb. is recognized over the analogous section *Seriphidium* Besser. Taxonomic treatment of species follows Beetle (1960) and Beetle and Young (1965).

Figure 1.--Differential grazing of two A. tridentata *subsp.* vaseyana *bushes in the Seeley Creek Drainage, Sanpete County, Utah.*

Chemotaxonomic methods have recently been used to study taxa within the *Tridentatae*. Chromatographic investigations by Holbo and Mozingo (1965), Young (1965), Winward and Tisdale (1969), Hanks and others (1971), and Brunner (1972) give support to the taxonomic treatment of species and subspecies by Hall and Clements (1923) and Beetle (Beetle 1960; Beetle and Young 1965). Identification and distribution of leaf phenols, sesquiterpene lactones, and alkanes are proving to be of value in delimitating *Artemisia* species (Shafizadeh and Melnikoff 1970; Shafizadeh and others 1971; Bachelor and others 1972).

Our special interest in sagebrush arose primarily from questions as to why game and livestock exhibited marked preferences for certain big sagebrush populations (Brunner 1972) or for certain individuals in a population (fig. 1). In earlier chromatographic work (Hanks and others 1971; Hanks and Jorgensen 1973), we reported evidence for and means of detecting some of these differences in subspecies of big sagebrush (*Artemisia tridentata* subsp. *tridentata* and *A. tridentata* subsp. *vaseyana*). In the course of this research, chromatographic analyses were done on other species in the *Tridentatae* as well. This paper stresses some considerable differences discovered among these species through chromatographic studies in 1969 and 1972, and outlines phylogenetic relationships among these species as suggested by chromatographic patterns. Other chromatographic analyses have been performed in the *Tridentatae*; however, this study is much broader in scope and builds on earlier work.

The large amount of genetic variation in natural populations of *Artemisia* provides wide opportunity for the development of improved races through artificial selection and breeding. Chromatography offers a rapid means of verifying the existence and extent of hybridization and also a technique for identifying types that would satisfy specific purposes.

EXPERIMENTAL PROCEDURES

Chromatographic analyses of more than 350 plant specimens are included in this study. The plants chromatographed came from widely occurring populations in Utah, Idaho, Nevada, Wyoming, Colorado, Arizona, Oregon, and British Columbia, and include most species of the section *Tridentatae*. Attempts were made to collect from a wide variety of sites so that collections would be fairly representative of the distribution of species and subspecies. Although the majority of collections were taken from sites within the Great Basin, many were obtained from populations outside this geographical area.

Artemisia populations were sampled by collecting foliage from mature representative individual bushes. Naturally occurring and transplanted bushes were sampled. Transplanting apparently did not affect the chromatographic patterns. Sampled foliage consisted of persistent, overwintering leaves from nonflowering stalks. Leaves on *Artemisia* flowering stalks have been reported to give variable results in chromatographic studies (Winward and Tisdale 1969; Brunner 1972). Early results indicated little seasonal variation in chromatographic patterns from persistent leaves; consequently, foliage was collected during all seasons of the year. Foliage was placed in open brown paper bags and dried at room temperature.

A modification of the chromatographic methods developed by Alston and Turner (1962) was employed. A mortar and pestle were used to pulverize 0.5 g. of dried leaves. Samples were placed in 30 ml. bottles into which 7.0 ml. absolute methanol had been introduced. Extraction of phenolic substances was carried out at room temperature for 24 hours. The extract then was decanted and concentrated by evaporation to 2.0 ml.

Twenty-five µl of this extract were added to duplicate 9-inch squares of Whatman No. 3 MM chromatographic grade filter paper. The solvent system for the first dimension was n-butanol:acetone:water (4:1:3) and for the second dimension, acetic acid:water (15:85). Chromatograms were viewed under longwave ultraviolet light before and after exposure to ammonia fumes in order to note the appearance and color changes of resulting spots. Each spot was given an arbitrary number for identification purposes and the R_f value computed for both dimensions of the finished chromatogram.

$$R_f = \frac{\text{Distance of spot from starting point}}{\text{Distance of solvent front from starting point}}$$

The R_f value of a given spot is then expressed as:

$$R_f = R_f(\text{first dimension})/R_f(\text{second dimension}).$$

Thin-layer plates coated with silica gel G were photographed to illustrate the difference among groups of big sagebrush. Each plate was divided into three 6- by 20-cm. sections and the base of each section was streaked with approximately 200 µl of extract. Chromatograms were developed in a single direction using n-butanol:acetone:water (4:1:1) as the solvent system. Following development, the plates were exposed to ammonia fumes, allowed to dry, and photographed under ultraviolet light (Kodachrome II film, ASA 25, and a 2B filter).

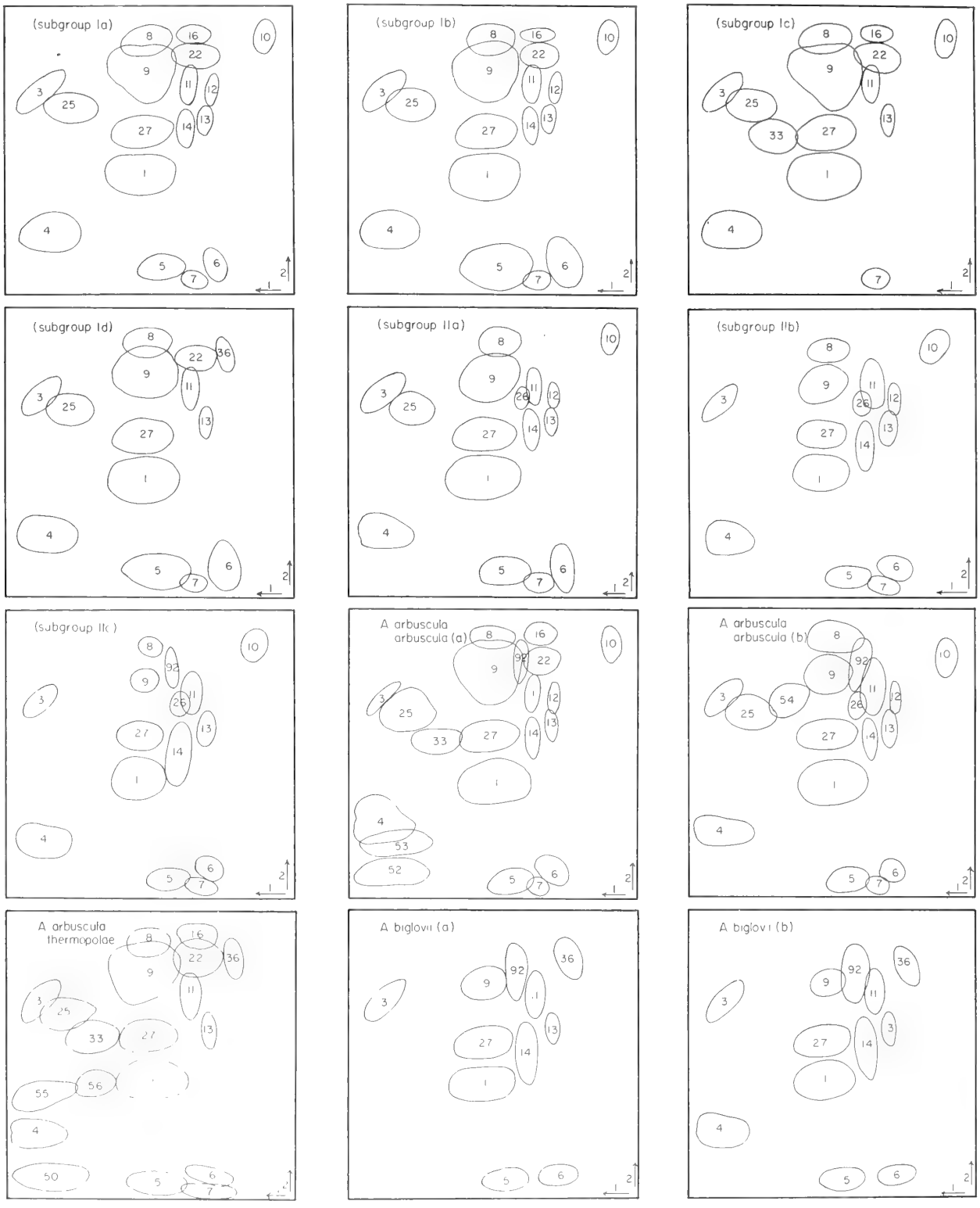
Identification of the constituents of the methanol extracts is beyond the scope of this paper. Shafizadeh and Melnikoff (1970) report that phenolic extractives of *Artemisia tridentata* subsp. *vaseyana* leaves are mainly coumarins with various side chain substituents.

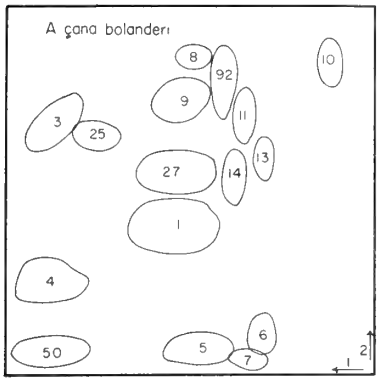
RESULTS

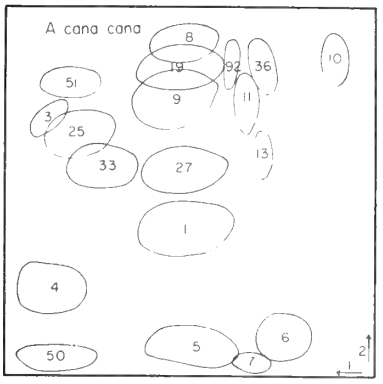
On the basis of chromatographic variations among collections of big sagebrush, the sources studied are divided into two major groups and seven subgroups (figs. 2-8 and table 1). Several of the chromatographic spots exhibited significant variations in size and intensity of color; so both qualitative and quantitative (table 2) variations were taken into consideration when the chromatograms were organized into groups. Characterization of chromatographic spots of big sagebrush by R_f values and colors (figs. 2-8 and table 2) is nearly identical with data presented in an earlier paper (Hanks and others 1971). The few changes represent judgments reached after further investigation, except for the R_f value of spot 4, which was misprinted in Hanks and others (1971). The missing numbers in the sequence (table 2) represent spots that appeared only occasionally in the chromatograms and, in most instances, provided no useful basis for the organization of the collections into groups. However, some of these might be indicative of past hybridization between big sagebrush and other sagebrush species.

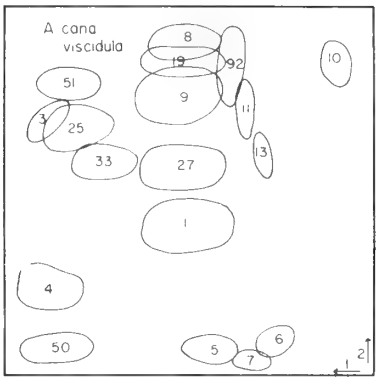
Variation within species or subspecies was also observed among other *Tridentatae* species. Representative chromatograms of each (i.e., *A. arbuscula* subsp. *arbuscula*, *A. arbuscula* subsp. *thermopolae*, *A. bigelovii*, *A. cana* subsp. *bolanderi*, *A. cana* subsp. *cana*, *A. cana* subsp. *viscidula*, *A. longiloba*, *A. nova*, *A. pygmaea*, *A. rigida*, *A. rothrockii*, *A. tripartita* subsp. *tripartita*) are illustrated in figures 9-25. Distribution of chromatographic spots among each is included in table 1. R_f values and color variations of the individual spots are given in table 2.

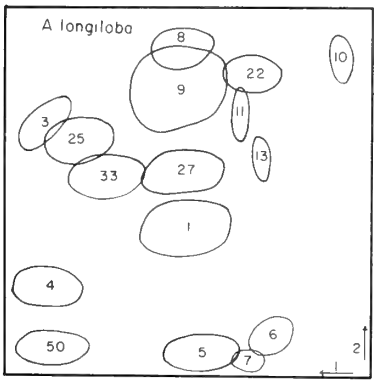
Figures 2-25.--Representative two-dimensional chromatograms of methanol-soluble extracts from the leaves of the subgroups of A. tridentata *(figs. 2-8) and other species of section* Tridentatae *(figs. 9-25). For spot coloration and* R_f *values, see table 2.*

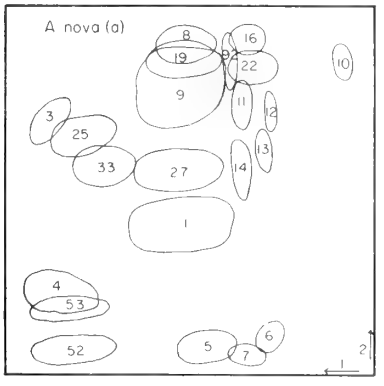


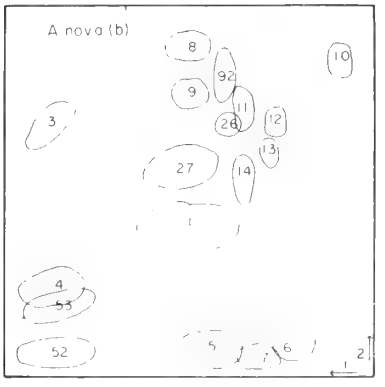

A çana bolanderi

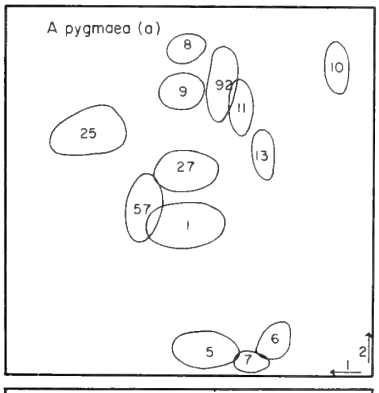

A cana cana

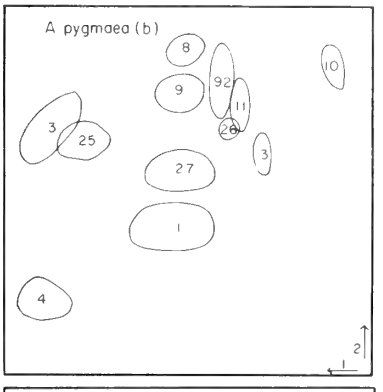

A cana viscidula

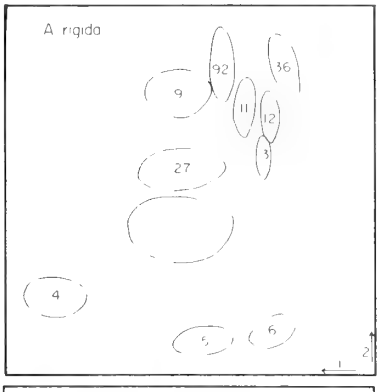

A longiloba

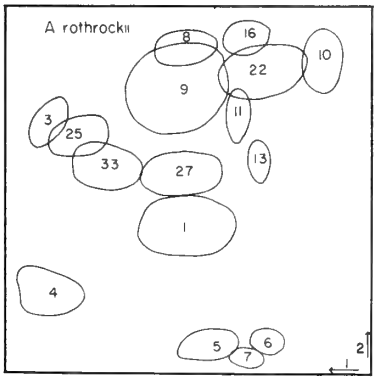

A nova (a)

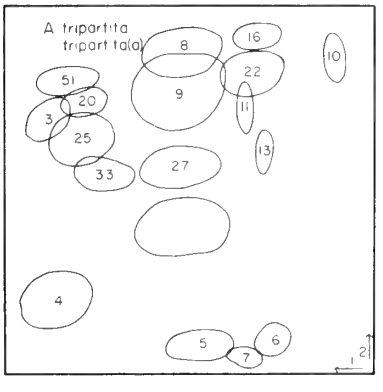

A nova (b)


A pygmaea (a)


A pygmaea (b)


A rigida


A rothrockii


A tripartita
tripartita(a)

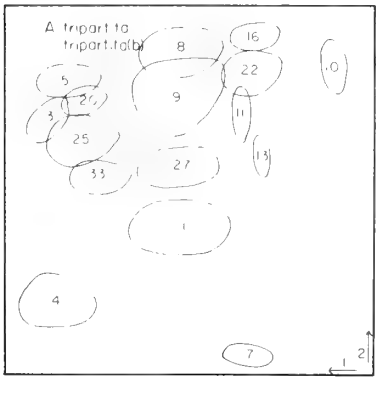

A tripartita
tripartita(b)

Table 1.--*Distribution of chromatographic spots among subgroups of* A. tridentata *and other* Artemisia *species.*[1]

Species and/or subspecies	Sub-group	Spot Number																														
		1	3	4	5	6	7	8	9	10	11	12	13	14	16	19	20	22	25	26	27	33	36	50	51	52	53	54	55	56	57	92
A. tridentata																																
subsp. *vaseyana*	Ia	+	+	+	1	1	+	+	5	+	+	+	+	+	+	-	-	+	+	-	+	-	-	-	-	-	-	-	-	-	-
subsp. *vaseyana*	Ib	+	+	+	5	5	+	+	4	+	+	+	+	+	+	-	-	+	+	-	+	-	-	-	-	-	-	-	-	-	-	-
subsp. *vaseyana*	Ic	+	+	+	-	-	+	+	5	+	+	-	+	-	+	-	-	+	+	-	+	+	-	-	-	-	-	-	-	-	-	-
subsp. *wyomingensis*	Id	+	+	+	4	4	+	+	4	-	+	-	+	-	-	-	-	+	+	-	+	-	+	-	-	-	-	-	-	-	-	-
subsp. *tridentata*	IIa	+	+	+	2	2	+	+	3	+	+	+	+	+	-	-	-	-	+	+	+	-	-	-	-	-	-	-	-	-	-	-
subsp. *tridentata*	IIb	+	+	+	2	2	+	2	2	+	+	+	+	+	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-
subsp. *tridentata*	IIc	+	+	+	2	2	+	1	1	+	+	-	+	4	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	+
A. arbuscula																																
subsp. *arbuscula*	(a)	+	1	4	2	2	+	+	5	+	+	+	+	+	+	-	-	+	4	-	+	+	-	-	-	+	+	-	-	-	-	+
subsp. *arbuscula*	(b)	+	+	+	2	2	+	4	2	+	+	+	+	+	-	-	-	-	+	+	+	-	-	-	-	-	-	+	-	-	-	+
subsp. *thermopolae*		+	+	+	1	1	5	+	4	-	+	-	+	-	+	-	-	+	+	-	+	+	+	+	-	-	-	-	+	+	-	-
A. biglovii	(a)	+	+	-	2	2	-	-	1	-	+	-	+	4	-	-	-	-	-	-	+	-	+	-	-	-	-	-	-	-	-	+
A. biglovii	(b)	+	+	+	2	2	-	-	1	-	+	-	+	4	-	-	-	-	-	-	+	-	+	-	-	-	-	-	-	-	-	+
A. cana																																
subsp. *bolanderi*		+	4	+	2	2	+	1	2	+	+	-	+	+	-	-	-	-	1	-	+	-	-	+	-	-	-	-	-	-	-	+
subsp. *cana*		+	2	+	4	4	+	4	3	+	+	-	+	-	-	4	-	-	4	-	+	+	+	+	+	-	-	-	-	-	-	1
subsp. *viscidula*		+	2	+	1	1	+	4	3	+	+	-	+	-	-	4	-	-	4	-	+	+	-	+	+	-	-	-	-	-	-	+
A. longiloba		+	+	+	2	2	+	+	5	+	+	-	+	-	-	-	-	+	+	-	+	+	-	+	-	-	-	-	-	-	-	-
A. nova	(a)	+	+	+	2	2	+	+	5	+	+	+	+	+	+	4	-	+	+	-	+	+	-	-	-	+	+	-	-	-	-	+
A. nova	(b)	+	+	+	2	2	+	+	2	+	+	+	+	+	-	-	-	-	-	+	+	-	-	-	-	+	+	-	-	-	-	+
A. pygmaea	(a)	+	-	-	2	2	+	1	1	+	+	-	+	-	-	-	-	-	4	-	+	-	-	-	-	-	-	-	-	-	+	+
A. pygmaea	(b)	+	4	+	-	-	-	1	1	+	+	-	+	-	-	-	-	-	2	+	+	-	-	-	-	-	-	-	-	-	-	+
A. rigida		+	-	1	+	+	-	-	1	-	+	4	+	-	-	-	-	-	-	-	+	-	+	-	-	-	-	-	-	-	-	+
A. rothrockii		+	+	+	2	2	+	+	5	+	+	-	+	-	+	-	-	4	+	-	+	+	-	-	-	-	-	-	-	-	-	-
A. tripartita																																
subsp. *tripartita*	(a)	+	2	4	1	1	+	5	4	+	+	-	+	-	+	-	+	4	+	-	+	+	-	-	+	-	-	-	-	-	-	-
subsp. *tripartita*	(b)	+	2	4	-	-	+	5	4	+	+	-	+	-	+	-	+	4	+	-	+	+	-	-	+	-	-	-	-	-	-	-

[1] + = characteristically present; - = characteristically absent; the numerals 1-5 represent relative brilliance of spots that exhibit significant variation in size and intensity of color, e.g., 1 = very dim and small, 3 = average size and color intensity, 5 = very large and brightly colored.

Table 2.--*R_f values and color of the chromatographic spots in* Artemisia *species*

Spot no.	R_f	Color		
		Ultraviolet	NH_3 + ultraviolet	NH_3 + daylight
1	0.53/.46	Blue	Yellow-green	Gray
3	.88/.71	Blue-green	Blue-green	--
4	.87/.29	Violet	Violet-brown	Yellow
5	.47/.11	Yellow or yellowish-brown	Yellow or yellowish-brown	--
6	.28/.13	Yellow or yellowish-brown	Yellow or yellowish-brown	--
7	.32/.08	Violet	Violet	Yellow-brown
8	.51/.87	Dark blue	Dark blue	--
9	.54/.78	Bright, iridescent blue	Bright, iridescent blue	--
10	.18/.84	--	Blue	--
11	.34/.75	Blue	Yellow-green	Yellow
12	.26/.71	--	Blue-violet	--
13	.29/.64	Pink	Yellow-pink	--
14	.35/.59	Blue (Violet in IIc)	Gray-blue (Violet in IIc)	--
16	.32/.90	Dark blue	Dark blue	--
19	.50/.83	--	Orange	--
20	.80/.73	--	Orange	--
22	.32/.84	Blue	Blue-green	--
25	.83/.67	Blue-green	Blue-green	--
26	.38/.73	Blue	Blue	--
27	.51/.57	Blue	Yellow-green	Gray
33	.75/.60	Pinkish-white	Pink	--
36	.26/.84	Blue	Blue	--
50	.78/.07	Brownish-gold	Brownish-gold	--
51	.85/.79	--	Yellow-green	--
52	.85/.12	Brownish-violet	Brownish-violet	--
53	.85/.19	Brownish-violet	Brownish-violet	--
54	.67/.76	--	Blue-green	--
55	.87/.41	Violet	Blue-violet	--
56	.71/.42	--	Tan	--
57	.57/.53	Violet	Violet	--
92	.42/.82	Blue	Blue-green	--

Table 3.--*Color of extract from each of seven subgroups of* A. tridentata *under ultraviolet light*

Subgroup	Color of extract under ultraviolet light
vaseyana Ia	Bluish-white to light blue
vaseyana Ib	Bluish-green to bluish-violet
vaseyana Ic	Creamy-white to bluish-white
wyomingensis Id	Brownish-violet to greenish-violet
tridentata IIa	Bluish-violet to greenish-violet
tridentata IIb	Greenish-violet
tridentata IIc	Violet to reddish-violet

Comparisons of single-dimension, thin-layer chromatograms of the seven subgroups of *A. tridentata* are shown in figures 26-32.

Another rapid, but less accurate, method of separating collections of big sagebrush into the previously described groups was detected during the course of the study. Viewed directly under ultraviolet light, methanol extracts fluoresce in distinctive colors based on the relative brilliance of the phenolic substances already described in the chromatographic analysis (table 3). Young (1965), Winward (1970), and Brunner (1972) have used thin-layer chromatography to distinguish *Artemisia* taxa.

The chromatographic spots that exert the greatest influence on composite coloration are 9, 5, and 6. Where spot 9 is large and brilliantly iridescent and 5 and 6 are only lightly colored (*vaseyana* Ia and *vaseyana* Ic), the extract is a brilliant creamy-white to bluish-white. However, when spots 5 and 6 are brilliantly colored (*vaseyana* Ib and *wyomingensis* Id), much of the brilliance of 9 is masked. In such cases, the composite color reflects the yellow of these spots and produces varying shades of brownish- and greenish-violet. In group II, where the intensity of spot 9 is much reduced, a corresponding reduction in the blue coloration of the composite mixture occurs that results in a strong violet background. The usefulness of this technique lies in the fact that the group to which big sagebrush belongs can be determined a few hours after collection. Since this determination is only qualitative, extraction of the leaves can begin at the time of collection, thus eliminating the drying time necessary for a more quantitative analysis. Winward and Tisdale (1969) outline a similar technique.

The same method also appears to be effective with seed. Methanol or water extract of big sagebrush seed from each subgroup fluoresces in colors similar to but less intense than those from corresponding foliar material. Consequently, it is a relatively simple procedure to determine the subspecies from which seed was harvested (Taylor and others 1964; Hanks and Jorgensen 1973).

Figures 26-32.--Color photographs of representative thin-layer chromatograms of the methanol-soluble extracts from the leaves of the seven subgroups of A. tridentata. *The origin is on the left. The bright red band near the solvent front (right) is chlorophyll A. Fig. 26, subsp.* vaseyana *subgroup Ia; fig. 27, subsp.* vaseyana *subgroup Ib; fig. 28, subsp.* vaseyana *subgroup Ic; fig. 29, subsp.* wyomingensis *subgroup Id; fig. 30, subsp.* tridentata *subgroup IIa; fig. 31, subsp.* tridentata *subgroup IIb; fig. 32, subsp.* tridentata *subgroup IIc.*

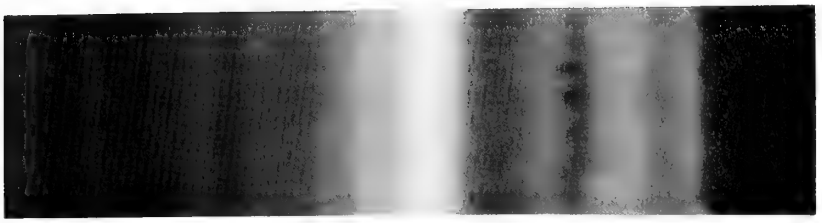


Figure 26
Ia

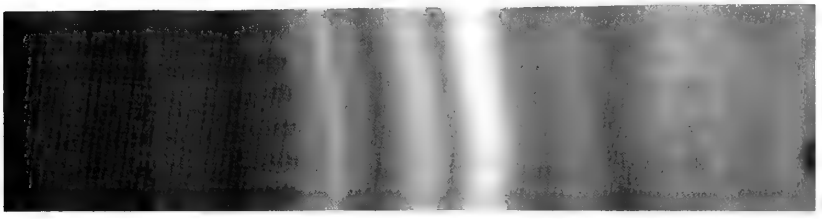


Figure 27
Ib

Figure 28
Ic

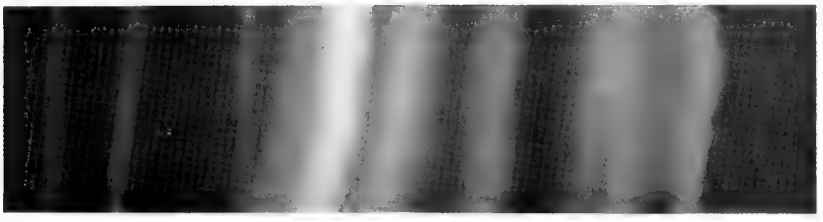


Figure 29
Id

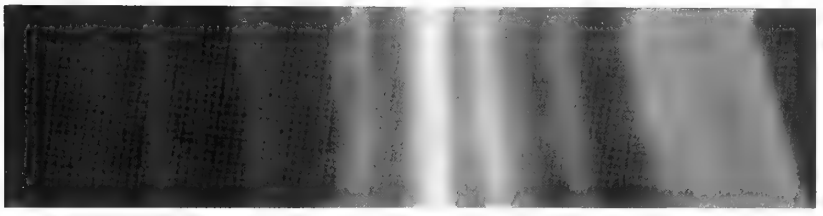


Figure 30
IIa

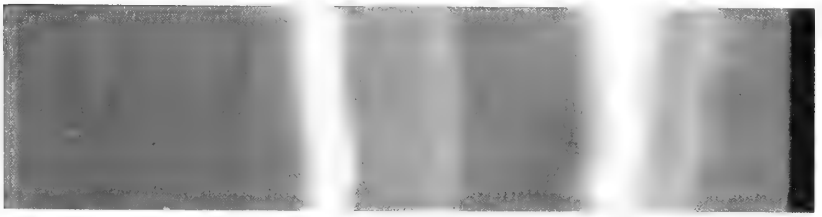


Figure 31
IIb

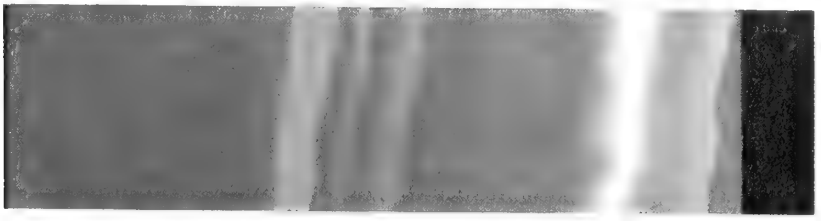


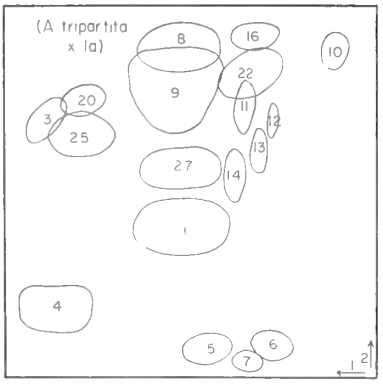
Figure 32
IIc

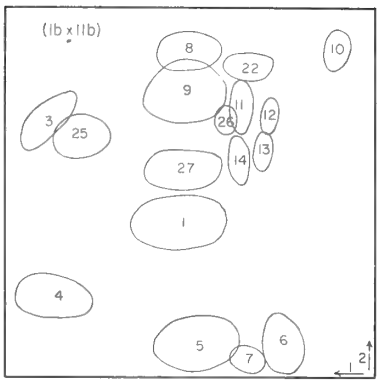
DISCUSSION

Evidence for the great plasticity of the *Tridentatae* complex and particularly of big sagebrush, suggested by Hall and Clements (1923) and further demonstrated by the cytogeographic studies of Ward (1953), is substantiated by the large number of chromatographic variants resulting from this study.

Greatest chromatographic variation was observed among collections of big sagebrush; at least seven rather distinct patterns were identified. Considerable additional variation was found among individual chromatograms of collections of this species, but these could not be associated with meaningful patterns. Similar multiple patterns (table 1) and incidental variation were found among collections of other species and subspecies, but none of these approached the apparent chemical diversity of *A. tridentata*.

The most common departure from regular chromatographic patterns seemingly resulted from interbreeding between *Tridentatae* species or subspecies. Chromatograms of progeny from naturally occurring hybrids could be identified by the appearance of spots specific for one parent species in the otherwise normal chromatogram of another species. The most common example of this phenomenon was the occurrence of traces of spot 19 from *A. nova* or *A. cana* subsp. *viscidula* in approximately one-fourth of the *A. tridentata* subsp. *tridentata* and *vaseyana* collections. In support of this contention, Beetle (1960) reported considerable evidence of *A. nova* in the morphological characteristics of big sagebrush populations on the Shivwitts Indian Reservation, Washington County, Utah. Chromatograms of collections from this vicinity, which were included in this study, contained a rather prominent spot 19, which supports Beetle's observation as to close relationship of this form to *A. nova*. Further evidence of past hybridization was the appearance of spot 20, specific for *A. tripartita* subsp. *tripartita* in approximately 20 percent of the collections of subgroup Ia of *A. tridentata vaseyana* (fig. 33). This spot was observed in widely scattered populations of subgroup *vaseyana* Ia from southwestern Idaho to southern Utah. Usually, the introgression shown by chemical patterns





Figures 33-34.--Representative two-dimensional chromatograms of methanol-soluble extracts from the leaves of putative hybrids A. tripartita *X* A. tridentata *subsp.* vaseyana *subgroup Ia (fig. 33) and* A. tridentata *subsp.* vaseyana *subgroup Ib X* A. tridentata *subsp.* tridentata *subgroup IIb (fig. 34).*

could not be associated with morphological characteristics. This type of introgression has wide distribution within the sagebrush populations. Collections taken from ecotones between populations of different species, subspecies, or ecotypes frequently express both morphological and chromatographic evidence of interbreeding.

Chromatographic evidence for hybridization between the following taxa was observed: *A. tridentata* subsp. *vaseyana* X *A. tridentata* subsp. *tridentata; A. tridentata* subsp. *vaseyana* X *A. arbuscula* subsp. *arbuscula; A. tridentata* subsp. *vaseyana* X *A. nova, A. tridentata* subsp. *vaseyana* X *A. tripartita* subsp. *tripartita*; *A. tridentata* subsp. *vaseyana* X *A. cana* subsp. *viscidula; A. tridentata* subsp. *tridentata* X *A. tripartita* subsp. *tripartita; A. cana subsp. viscidula* X *A. tripartita* subsp. *tripartita*. Examples are illustrated in figures 33 and 34. We are confident that many others will come to light as this technique is more widely applied.

Ecological distribution.--The following observations have been made regarding the ecological distribution of the chromatographic groups of big sagebrush, primarily within the Great Basin. Collections of Group I (*Artemisia tridentata* subsp. *vaseyana* and subsp. *wyomingensis*) have come mostly from mountain habitats extending from the upper elevational limits of the big sagebrush zone to, and slightly beyond, the base of the foothills. Specimens of *vaseyana* Ic, which were all collected from the upper elevations of the big sagebrush zone, appear to be widely distributed, as is evidenced by collections of this subgroup (*vaseyana* Ic) from Utah, Idaho, Nevada, Wyoming, and Colorado. *Vaseyana* Ic may include *A. tridentata* subsp. *vaseyana* f. *spiciformis* (Beetle 1960; Winward 1970). The distribution of *vaseyana* Ia extends downward from the *vaseyana* Ic zone to the lower foothills, overlapping considerably with *vaseyana* Ic in the upper elevations and *vaseyana* Ib in the foothills. Subgroup *vaseyana* Ib predominates in the lower foothill pinyon-juniper zone and extends into peripheral lowland areas where it overlaps with *tridentata* IIb. It is interesting that Winward (1970) recognized an analogous or perhaps identical taxon to our *vaseyana* Ib in his taxonomic and ecological study of Idaho big sagebrush. He tentatively referred to this taxon as *A. tridentata* subsp. *vaseyana* f. *xericensis*. However, that name has not been validly published (Winward 1970).

Subgroup *wyomingensis* Id (which occurs in Wyoming, Montana, southern Idaho, northern Nevada, and northern Colorado) overlaps *vaseyana* Ib, the lower end of *vaseyana* Ia, and to a greater extent, the upper end of *tridentata* IIb. Beetle and Young (1965) maintain that *A. tridentata* subsp. *wyomingensis* is intermediate in ecology, morphology, and distribution between *A. tridentata* subsp. *vaseyana* and *A. tridentata* subsp. *tridentata*. Our chromatographic data (table 1) support their recognition of subsp. *wyomingensis* as a valid separate subspecies and corroborate Young's (1965) thin-layer chromatographic evidence for three subspecies. However, our data indicate that subsp. *wyomingensis* has closer affinities to subsp. *vaseyana* than to subsp. *tridentata*.

Table 4.--*Flowering dates of the chromatographic subgroups of* A. tridentata

Subgroup	Flowering date
vaseyana Ic	July 15-30
vaseyana Ia	August 5-20
vaseyana Ib	September 7-21
wyomingensis Id	September 7-21
tridentata IIa	September 7-21
tridentata IIb	September 10-October 10
tridentata IIc	September 10-October 10

One of the primary genetic modifications necessary to permit the development of short-growing-season strains in high elevations is the ability to reproduce under prevailing conditions. Of interest in this regard is the early flowering of *vaseyana* Ic and *vaseyana* Ia in contrast to the other subgroups. All seven subgroups are growing together at Snow College Field Station, Ephraim, Utah (5,600 feet elevation). Here, *vaseyana* Ic blooms as early as mid-July and *vaseyana* Ia by early August, whereas the other subgroups are not in flower until after the first week of September (table 4). Phenological data presented here are in general agreement with observations from uniform gardens in northern Idaho (Winward 1970) and south central British Columbia (Marchand and others 1966). The Canadian investigators found, as we did, early- and late-flowering ecotypes of *A. tridentata* subsp. *vaseyana*.

The dominant low-elevation valley big sagebrush (*A. tridentata* subsp. *tridentata*) of the northern Great Basin is *tridentata* IIb; in the southern Great Basin, however, *tridentata* IIc is the common low-elevation valley big sagebrush. Small populations of IIc can frequently be seen throughout the Great Basin as tall shrubs growing along fence rows or in other protected areas. *Tridentata* IIb predominates in most low-elevation big sagebrush sites, but it is not confined to these areas; it can be found elsewhere in small populations intermixed with *vaseyana* Ia and *vaseyana* Ib types, particularly in the lower foothill areas.

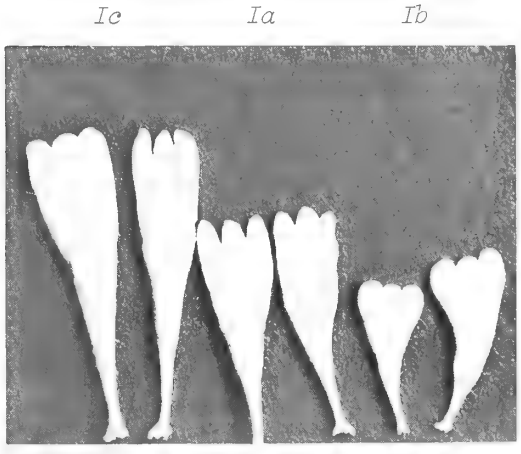
Subgroup *tridentata* IIa was collected only from localized areas of northwestern Nevada where it grows in close association with *A. tridentata* subsp. *wyomingensis* (Id). In fact, chromatographically, it appears to have arisen from hybridization between *wyomingensis* Id and *tridentata* IIb since it contains characteristics common to both (fig. 6).

There is abundant chromatographic evidence that where populations of subgroups overlap and intermix, interbreeding occurs. This is particularly evident in ecotonal areas between populations of *vaseyana* Ib and *tridentata* IIb; chromatograms of many specimens contain unusual combinations of spots not found in isolated, uniform populations of either subgroup (fig. 34).

The distribution of subgroups is so uniform within the Great Basin that rather accurate predictions as to their presence can frequently be made after considering elevation and topography. However, distribution outside this area appears to be more erratic. For instance, only a few specimens of subgroup *vaseyana* Ib have been collected from areas peripheral to the Great Basin. Collection sites outside this area, physically similar to those within the Great Basin in which this subgroup is characteristic, are usually occupied by *vaseyana* Ia, the most widely distributed of the *A. tridentata* subsp. *vaseyana* subgroups. Furthermore, *A. tridentata* subsp. *wyomingensis*, widely

distributed in Wyoming and Montana (Beetle and Young 1965) and extending into Idaho and Northern Nevada, is not common within the Great Basin. Brunner (1972) noted a different ecotype of subsp. *wyomingensis* in the Great Basin. Additional evidence of this change in distribution patterns is the fact that most populations of subspecies *tridentata* in these same peripheral areas bear more chromatographic similarity to *tridentata* IIc than to *tridentata* IIb, even though these populations occupy areas similar to those occupied by *tridentata* IIb within the Great Basin. This conclusion is based on collections from eastern Utah, southern Idaho, and parts of Wyoming.

Morphological aspects.--While a thorough morphological study of the seven subgroups of big sagebrush has not been made, the following observations have been noted. The subgroups Ia, Ib, and Ic are undoubtedly variations within the subspecies *vaseyana*. The distribution, the spatulate or broadly cuneate leaf shape (fig. 35), and the pleasant mintlike fragrance of the specimens within these subgroups are all characteristic



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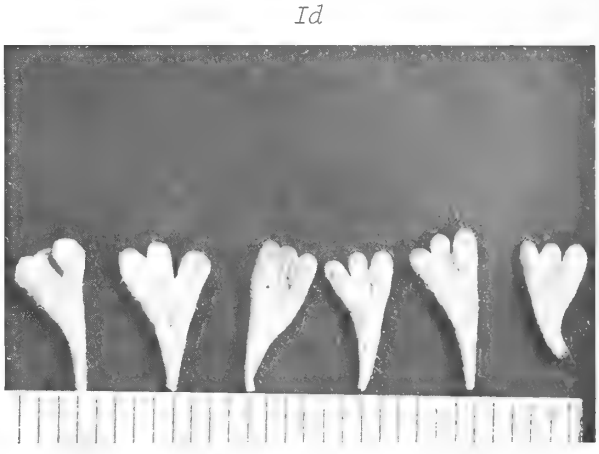

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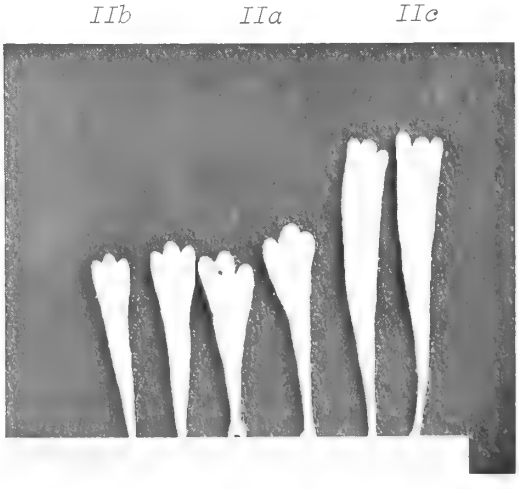

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Figures 35-37.--Photographs of representative leaves of the chromatographic subgroups of A. tridentata *(scale is in mm). Fig. 35, from left to right, subgroups Ic, Ia, and Ib of subspecies* vaseyana*; fig. 36, subspecies* wyomingensis*; fig. 37, from left to right, subgroups IIb, IIa, and IIc of subspecies* tridentata.

of descriptions reported for the subspecies *vaseyana*. However, there seems to be little morphological difference between Ia, Ib, and Ic that can be used consistently to separate them. Odor differences are not sufficiently characteristic to distinguish groups within subspecies. Considerable variation in leaf color has been observed, but similar shades can be found in each subgroup. Leaf size appears to be slightly reduced from Ic to Ia to Ib as the elevation decreases (fig. 35). However, this is believed to be mostly a reflection of the favorability of the site since the difference does not always persist when all types are grown under similar environmental conditions. Leaves of subgroup Id (*A. tridentata* subsp. *wyomingensis*) are cuneate in form and are the smallest in group I (fig. 36).

Similarly, IIa, IIb, and IIc are probably different ecotypes within the subspecies *tridentata*. Leaves of IIa and IIb are cuneate, whereas those of IIc are longer and oblanceolate (fig. 37). Subgroups IIa and IIb appear to be morphologically similar. However, differences have been observed between them and IIc. Plants of subgroup IIc are commonly observed along fence rows, gullies, and similar places throughout the northern Great Basin, but are more common to the south. These plants are typically much taller than those of IIa and IIb, frequently attaining heights of 12 to 15 feet. Although individual plants of large populations of IIc are not generally as tall as those growing along fence rows or in other protected places, they are somewhat taller than similar populations of IIa or IIb. The color of IIc is quite distinct and individuals of this group can usually be distinguished from IIa and IIb by observers acquainted with color variations in sagebrush populations. Plants of subgroups IIa and IIb usually exhibit varying shades of gray green, whereas those of IIc are bluish gray.

The collections studied may not have included representatives from either *A. tridentata* subsp. *vaseyana* f. *spiciformis* or *A. tridentata* subsp. *tridentata* f. *parishii* (Beetle 1960). However, a few long-leafed, high-elevation specimens of *A. tridentata* subsp. *vaseyana* were chromatographed. These collections were chromatographically similar to shorter-leafed *A. tridentata* subsp. *vaseyana* types and are included in *vaseyana* Ic. Furthermore, plants of large stature with drooping inflorescences, a prominent characteristic of *A. tridentata* subsp. *tridentata* f. *parishii*, were collected from the sandy areas of northwestern Nevada. Most of these were chromatographically similar to *tridentata* IIa. We have assumed that these were probably not true *A. tridentata* subsp. *tridentata* f. *parishii* collections.

Distribution in relation to grazing preference.--The two major chromatographic groups, I and II, also show a pronounced difference in palatability. Almost without exception, collections from individual shrubs or populations that normally show signs of heavy grazing by deer and livestock, especially on winter ranges, are included in group I. Grazing preference has been evident for many plants collected from widely scattered areas under heavy utilization at the time of collection. On the other hand, all collections from populations observed to be relatively unpalatable are included in group II. The preference for group I plants, as contrasted with those of group II, was particularly evident in the area from which *wyomingensis* Id and *tridentata* IIa were collected in Nevada and where these two types were growing together as an intermixed population. Form *wyomingensis* Id was highly palatable to cattle that grazed the area, but form *tridentata* IIa was grazed very little. Sheep and deer exhibited the same partiality for *wyomingensis* Id. Similar selectivity of group I over group II has been observed where types *vaseyana* Ib and *tridentata* IIa come together and intermix in lower foothill areas in the Great Basin. Under these circumstances, plants of *vaseyana* Ib are grazed much more extensively than those of *tridentata* IIb. Intermediates resulting from apparent hybridization between these two strains exhibit considerable variation in the degree to which they are grazed, but are usually preferred to the group II plants.

Table 5 illustrates the differential browsing selectivity of deer during April of 1972 for the foliage of several sources from different intermountain areas. Plants from

Table 5.--Utilization by deer of transplanted A. tridentata *on winter range near Price, Carbon County, Utah*

Accession no.	Place of origin	Subspecies	Subgroup	Percent utilization
1601	Hobble Creek, Utah Co., Utah	*vaseyana*	Ia	60
2201	Indian Peaks, Beaver Co., Utah	*vaseyana*	Ia	45
4801	Soldier's Summit, Wasatch Co., Utah	*vaseyana*	Ia	65
5701	Wallsberg, Wasatch Co., Utah	*vaseyana*	Ib	70
6302	Leonard Creek, Humboldt Co., Nevada	*vaseyana*	Ib	95
6301	Leonard Creek, Humboldt Co., Nevada	*wyomingensis*	Id	90
3601	Trough Springs, Humboldt Co., Nevada	*tridentata*	IIa	35
1501	Indianola, Sanpete Co., Utah	*tridentata*	IIb	35
1701	Black Mountain, Sevier Co., Utah	*tridentata*	IIb	10
1703	South of Manti, Sanpete Co., Utah	*tridentata*	IIb	10
2002	Marysvale, Piute Co., Utah	*tridentata*	IIb	20
4302[1/]	Gordon Creek, Carbon Co., Utah	*tridentata*	IIb	35
6704	Dove Creek, Dolores Co., Colorado	*tridentata*	IIb or IIc	30

[1/] The common, native big sagebrush on this winter range.

various sources were removed from their native habitats and transplanted into adjacent rows of about 100 plants each on Utah Division of Wildlife Resources deer winter range northwest of Price, Utah (fig. 38). This kind of planting reduces environmental factors (e.g., soil and climate) that might have a confounding infuence on utilization.

Although the degree that plants from one source were grazed varied considerably, a strong preference is indicated for group I-type plants as compared to group II-type plants (table 5, figs. 38 and 39). Older but similar plantings that have been grazed by deer and livestock over a longer period of time substantially confirm these observations. We have observed only one instance where grazing animals preferred group II to group I. This exception involved 40 group II plants transplanted from a lowland black greasewood area onto a foothill site having a prevailing group I population. In this instance, deer showed a marked preference for the group II plants. Possibly, the different taste of group II plants in a predominantly group I area attracted the deer.

Figure 38.--Photograph showing transplanted A. tridentata *for deer browsing selectivity experiments. Arrow, heavily browsed* A. tridentata *subsp.* vaseyana *subgroup Ia accession from Hobble Creek, Utah County, Utah; the two rows to right of arrow, unbrowsed* A. tridentata *subsp.* tridentata *subgroup IIb accession from Indianola, Sanpete County, Utah. Photograph taken January 1971. Note the deer tracks.*

Figure 39.--Photograph showing differential deer selectivity in browsing A. tridentata *from different sources. An* A. tridentata *subsp.* vaseyana *subgroup Ib is on the left and an* A. tridentata *subsp.* tridentata *subgroup IIb on the right.*

In summary, *wyomingensis* Id and *vaseyana* Ib are highly preferred, other *vaseyana* subgroups, Ia and Ic, are moderately preferred, and subspecies *tridentata* subgroups IIa, IIb, and IIc are least preferred by grazing animals.

Occasionally, single plants or small groups of plants within large populations of heavily grazed plants are grazed far less than the rest of the population. Several chromatographic analyses have been made when plants that possessed similar morphological characters have been found growing side by side, but one has been heavily grazed, the other ungrazed. In most instances, no important variations in chromatographic patterns were found. However, in collections of this type from lower *A. tridentata* subsp. *vaseyana* (Ib) elevations, chromatograms of the ungrazed plants frequently show evidence of hybridization with *A. tridentata* subsp. *tridentata*, which may account for the difference in selectivity.

Some evidence indicates that reduced brilliance of spot 9 and the appearance of spot 26 in *A. nova* (fig. 19) is also associated with decreased grazing preference. This apparent pattern has not been conclusively demonstrated for all sources. A similar change in chromatographic pattern was observed in *A. arbuscula* subsp. *arbuscula* (fig. 10), but no correlation could be drawn between this characteristic and utilization by game or livestock. Further observations will be required.

Phylogenetic relationships.--Hall and Clements (1923) postulated the evolution of the section *Tridentatae* from the more primitive section *Abrotanum*. They further believed that section *Tridentatae* first gained a foothold in the arid southwestern United States and later moved northward into the Great Basin as climatic conditions became favorable for its expansion into these areas. The connecting link between the sections *Abrotanum* and *Tridentatae* is probably *A. biglovii* (Hall and Clements 1923). *Artemisia biglovii* is a fairly abundant shrub in the upper Colorado and upper Rio Grande River drainages of Utah, Colorado, New Mexico, and Arizona. It produces ray-flowers characteristic of *Abrotanum* and also the trident leaves and overall general appearance peculiar to *Tridentatae*. Support for *A. biglovii*-like taxa as phylogenetic connectors between the two sections, *Tridentatae* and *Abrotanum*, is gained by *A. biglovii's* intermediate characteristics. Hall and Clements (1923), Ward (1953), and Holbo and Mozingo (1965) place *A. biglovii* in section *Abrotanum*, whereas Moss (1940) and Beetle (1960) place it

in section *Tridentatae*. Chromatograms of *A. biglovii* express a marked resemblance to *Tridentatae* species while demonstrating less similarity toward species of *Abrotanum* (figs. 12, 13; unpublished data[2]). Consequently, its inclusion in *Tridentatae* is probably the more accurate arrangement and more indicative of its true relationship.

Hall and Clements (1923) also suggest that the parent big sagebrush to evolve from *A. biglovii* was probably *A. tridentata* subsp. *typica* (synonymous with subspecies *tridentata* as described by Ward (1953) and Beetle (1960) and as used in the present paper), principally because it appeared to have adapted to environmental conditions under which *A. biglovii* grew. Chromatographic evidence in the present study substantiates this view and suggests that the parental big sagebrush stock was probably subgroup *tridentata* IIc or unknown taxa having similar chromatographic characteristics to this subgroup (fig. 40). Chromatograms of *A. biglovii* and subgroup *tridentata* IIc are strikingly similar. Spot 9 is small in both, although somewhat more brilliant in *A. biglovii*. Chromatograms of *A. biglovii* contain a large and intensely violet spot 14 and a bright blue-green spot 92. Of the seven chromatographic subgroups of big sagebrush, subgroup *tridentata* IIc alone exhibits this same combination of spots. In all other subgroups, spot 14 is blue to blue-gray and not usually a prominent part of the chromatogram, and 92 is missing. Furthermore, the wide distribution of *tridentata* IIc-type plants in southerly localities where *A. biglovii* is also quite commonly found lends emphasis to the likelihood of a past connection between these two forms. Paradoxically, *A. biglovii* and *tridentata* IIc exhibit little morphological similarity. Biglow sagebrush is a diminutive form, erroneously called black sagebrush by many. In contrast, *tridentata* IIc contains the largest specimens in the section; plants occasionally reach 12 to 15 feet in height. Another significant point that we cannot account for is the fact that grazing animals show high preference for *A. biglovii*, but low preference for big sagebrush *tridentata* IIc.

Subgroup *vaseyana* Ia probably arose as an early variant of big sagebrush and probably represents the parent strain of the present-day subspecies *vaseyana* subgroups (fig. 40). The basis for this conclusion is the chromatographic similarity of this subgroup to other *Tridentatae* species. These include *A. nova*, *A. arbuscula*, *A. cana*, *A. tripartita*, *A. rothrockii*, and *A. longiloba*, all of which purportedly evolved from *A. tridentata*. The common occurrence of a brilliantly iridescent spot 9 in chromatograms of these sagebrush species suggests closer relationship to group I-type plants (*A. tridentata* subsp. *vaseyana* and subsp. *wyomingensis*) than to group II-types where spot 9 is small and exhibits little iridescence. Furthermore, considering the subgroups of group I, none bears greater chromatographic resemblance to these species than does *vaseyana* Ia. Consequently, subgroup *vaseyana* Ia seems to be the branch of big sagebrush arising from *tridentata* IIc and the branch from which other subgroups of group I and most of the section *Tridentatae* evolved. From *vaseyana* Ia-type plants, which occupy an intermediate elevational habitat, subgroups *vaseyana* Ib and *vaseyana* Ic probably arose as modifications respectively adapted to elevational zones below and above that of *vaseyana* Ia (fig. 40).

Artemisia tridentata subsp. *vaseyana* may have arisen before the establishment of big sagebrush within the Great Basin since this form occurs extensively throughout the present range of the *A. tridentata* complex. However, the range of *vaseyana* Ib is largely restricted to habitats within the Great Basin; so this ecotype probably originated within this geographical area.

Our data coupled with that of Beetle and Young (1965) support the hypothesis that *A. tridentata* subsp. *wyomingensis* is derived from subspecies *vaseyana* and *tridentata* of *A. tridentata* and ancestral stock not unlike *vaseyana* subgroups Ia and/or Ib and *tridentata* subgroups IIb and/or IIc (fig. 40).

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[2]David Hanks. 1969 chromatography information on file at Intermountain Forest and Range Experiment Station, Ephraim, Utah.

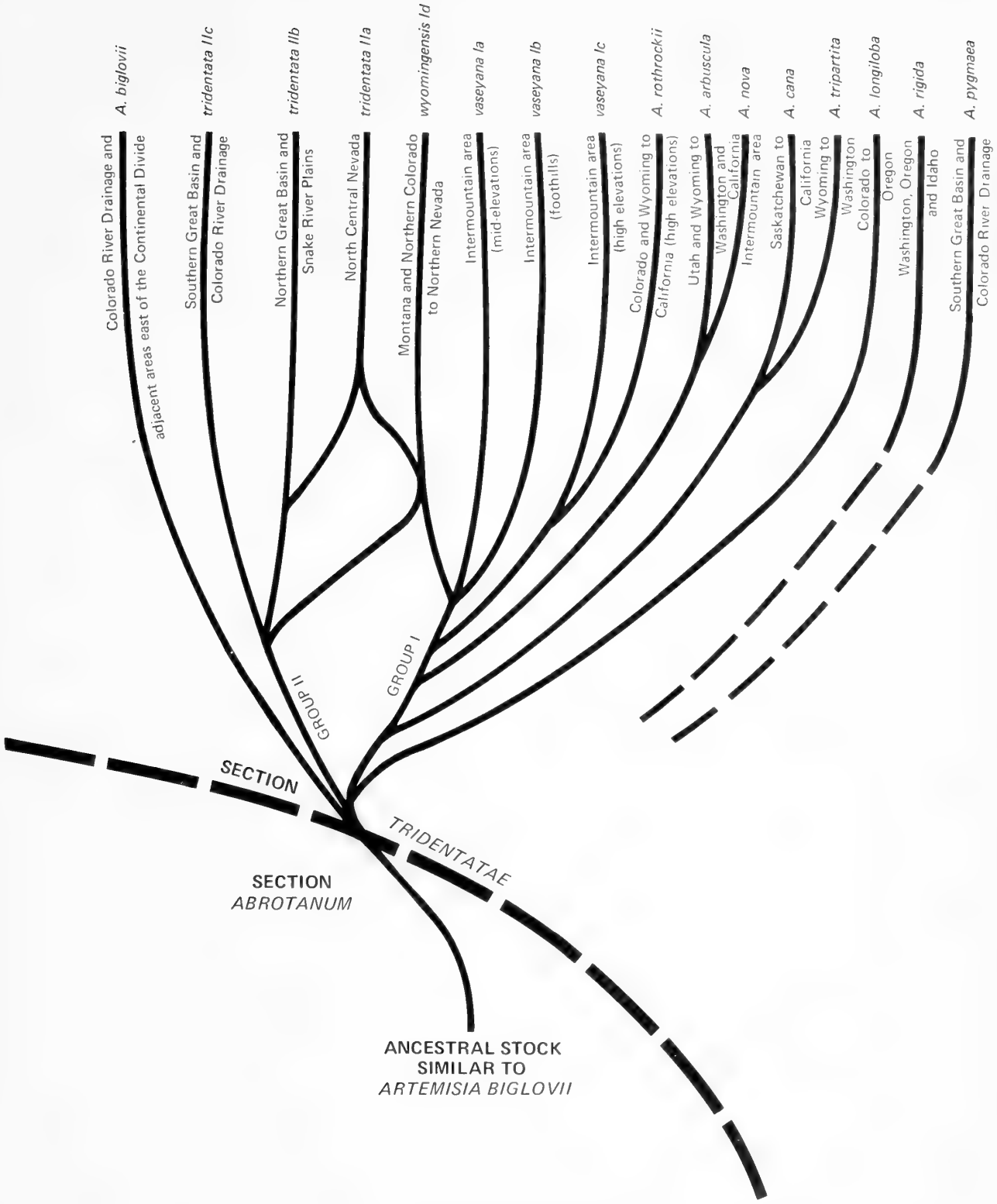

Figure 40.--A phylogenetic tree based mostly upon chromatographic patterns reported herein, but also upon the studies of Hall and Clements (1923), Ward (1953), Beetle (1960), and Beetle and Young (1965).

Based on cytological evidence, Taylor and others (1964) postulated the evolution of *A. tridentata* subsp. *tridentata* from *A. tridentata* subsp. *vaseyana* for the British Columbia populations of these two subspecies. In British Columbia, *A. tridentata* subsp. *vaseyana* populations are uniformly diploid, $n = 9$, whereas *A. tridentata* subsp. *tridentata* are all tetraploid, $n = 18$. No introgression between subspecies was observed by Taylor and others (1964) in contrast to the relatively common introgressed populations of the Great Basin. In the Great Basin and adjacent areas, diploid and tetraploid populations of both subspecies occur (Ward 1953; Winward 1970; unpublished data[3]). No logical pattern of chromosomal evolution is apparent for the *Tridentatae* as a whole either in the Great Basin or over its complete range of distribution. A cytological study should help to clarify the evolutionary past of the Great Basin *Tridentatae*.

The phylogenetic pathway of taxa similar to *A. biglovii* ⟶ *tridentata* IIc ⟶ *vaseyana* Ia including evolutionary adaptive radiations from subgroups *tridentata* IIc and *vaseyana* Ia is suggested for the Great Basin *Tridentatae* by chromatographic evidence presented here (fig 40). Hybridization-polyploidization cycles such as exhibited in section *Tridentatae* result in reticulate evolutionary patterns (Ward 1953).

Artemisia nova, *A. arbuscula*, *A. cana*, and *A. tripartita* apparently represent two separate evolutionary lines from subgroups *vaseyana* Ia (fig. 40). The latter two species not only appear chromatographically similar to *vaseyana* Ia, but they largely occupy similar habitats. *Artemisia cana* and *A. tripartita* share a common chromatographic spot, 51, which is not found in other *Artemisia* species (table 1). Since it is unlikely that the same spot should have a separate origin in each, these species probably had a common unknown ancestor, or one evolved from *A. tridentata* subsp. *vaseyana* and became the parent of the second. Similar problems are encountered in determining the origin of *A. nova* and *A. arbuscula*. The common ancestry of these two species is suggested by spots 52 and 53, not contained in chromatograms of *A. tridentata* subsp. *vaseyana*, but present in chromatograms of both *A. nova* and *A. arbuscula* (table 1). The connecting link to *A. tridentata* subsp. *vaseyana* may be through either of these species or from an unknown ancestor. The older of these two lines is probably that of *A. cana* and *A. tripartita* since these species exhibit the greatest chromatographic dissimilarity to *A. tridentata* subsp. *vaseyana*. *Artemisia nova* and *A. arbuscula* are more similar to *A. tridentata* subsp. *vaseyana* and so may have more recent origin.

The striking similarity of chromatograms of *A. rothrockii* to those of *vaseyana* Ia and *vaseyana* Ic suggests a close relationship among them (table 1; figs. 2, 4, 23, and 40; Ward 1953; Beetle 1960). Therefore, this species must have evolved from one of the higher elevation subspecies *vaseyana* types, probably *vaseyana* Ic, since the elevational range of this subgroup is nearest that of *A. rothrockii*.

The relationship of *A. pygmaea* to other members of the section *Tridentatae* is not clear. Rydberg (1916) placed this species in a separate section, *Pygmaeae*, although more recent authors (Hall and Clements 1923; Ward 1953; and Beetle 1960) have considered it to be included in *Tridentatae*. Beetle (1960) suggests that it may have an early link with *A. nova*; however, chromatographically, there is no evidence of such a relationship. Chromatograms of this species bear greater resemblance to *A. biglovii* or subgroup *tridentata* IIc than to other *Tridentatae* species (fig. 21). The individual plants of the species tend to be dwarf and usually occur on severe sites impregnated by a fairly high degree of alkalinity.

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[3]E. Durant McArthur. *Artemisia* cytological data on file at Intermountain Forest and Range Experiment Station, Ephraim, Utah.

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U.S. GOVERNMENT PRINTING OFFICE: 1973 — 784-485 / 20 REGION NO. 8

HANKS, DAVID L., E. DURANT McARTHUR, RICHARD STEVENS, and A. PERRY PLUMMER

1973. Chromatographic characteristics and phylogenetic relationships of Artemisia, section Tridentatae, USDA For. Serv. Res. Pap. INT-141, 24 p., illus. (Intermountain Forest & Range Experiment Station, Ogden, Utah 84401.)

This study is a chromatographic analysis of the section Tridentatae of Artemisia. Seven chromatographic subgroups of A. tridentata are identified. These subgroups are correlated with ecological distribution, morphological characteristics, and animal grazing preference. The study includes representative chromatograms for most species of Tridentatae and a discussion and chart of the phylogeny of this section based on chromatographic patterns.

OXFORD: U545.844: 165.1. KEYWORDS: chromatography, phylogeny, Artemisia tridentata, A. arbuscula, A. biglovii, A. cana, A. longiloba, A. pygmaea, A. rigida, A. rothrockii, A. tripartita, palatability.

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Headquarters for the Intermountain Forest and Range Experiment Station are in Ogden, Utah. Field Research Work Units are maintained in:

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Reno, Nevada (in cooperation with University of Nevada)