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Cytogeography and chromosome evolution of subgenus *Tridentatae* of *Artemisia* (Asteraceae)[1]

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The subgenus *Tridentatae* of *Artemisia* (Asteraceae: Anthemideae) is composed of 11 species of various taxonomic and geographic complexities. It is centered on *Artemisia tridentata* with its three widespread common subspecies and two more geographically confined ones. Meiotic chromosome counts on pollen mother cells and mitotic chromosome counts on root tips were made on 364 populations ($\bar{X}$ = 3.1 plants per population). These population counts are ~60% of all *Tridentatae* counts. Some are first records for taxa. The *Tridentatae* are a polyploid complex (x = 9) with ploidy levels from $2x$ to $8x$, but mostly $2x$ (48%) and $4x$ (46%). Polyploidy occurs in nine of the 11 species and in many subspecies as well. Supernumerary or b chromosomes are present only at a low frequency. In the principal species, *A. tridentata,* $2x$ plants are larger than $4x$ ones, which are adapted to drier conditions, probably in consequence of their slower growth rates. Gigas diploidy is a phenomenon shared by some other woody genera, but is in contrast to the gigas polyploid nature of many herbaceous genera. Polyploidy occurs within populations and is essentially autoploid. Hybridization sometimes occurs at taxa interfaces in stable hybrid zones. Stable *Tridentatae* hybrid zones coupled with the group's inherent propensity for polyploidization has led to the establishment of a geographically and numerically large and successful complex of species.

Key words: *Artemisia*; Asteraceae; cytogeography; hybridization; polyploidy; sagebrush; *Seriphidium*; *Tridentatae*.

The sagebrushes of western North America (= subgenus *Tridentatae* of *Artemisia*) are landscape-dominant plants (Küchler, 1964; West, 1983a, b). They are among, if not, the most common plants in terms of area occupied and number of individual plants in the United States from Canada to Mexico west of 100° west longitude.

Traditionally, the subgeneric taxonomy of *Artemisia* follows a system established by Besser (1829) wherein he separated sections based on various combinations of disc and ray flower occurrences and fertility. Besser's four sections (*Abrotanum, Absinthium, Dracunculus,* and *Seriphidium*) have been modified by subsequent workers. Rydberg (1916) elevated the sections to subgenera and created subordinate sections including section *Tridentatae* for the North American members of subgenus *Seriphidium.* Current consensus is to recognize three subgenera: *Artemisia* L. (= Bessers's *Abrotanum* + *Absinthium*), *Dracunculus* (Besser) Rydb., and *Seriphidium* (Besser) Rouy. However, McArthur, Pope, and Freeman (1981), based on karyotypic, chemotaxonomic, and distributional criteria, elevated *Tridentatae* to subgeneric status as *Tridentatae* (Rydb.) McArthur inclusive of 11 species (*A. arbuscula, A. argillosa, A. bigelovii, A. cana, A. longiloba, A. nova, A. pygmaea, A. rigida, A. rothrockii, A. tridentata,* and *A. tripartita*). Several authors, e.g., Barker and McKell (1983, 1986), Shultz (1983, 1986), and Wilt et al., (1992), have accepted this proposal. Others, e.g., Kornkven, Watson, and Estes (1998), have opted to treat *Tridentatae* at the sectional level. Big sagebrush (*A. tridentata*) with its three common subspecies (*tridentata, vaseyana,* and *wyomingensis*) and two less common ones (*spiciformis* and *xericensis*) is, by far, the most widespread and common species. Several other species and their subspecific entities, e.g., *A. arbuscula, A. cana,* and *A. nova,* are also widespread and ecologically important (Beetle, 1960; Goodrich, McArthur, and Winward, 1985; Rosentreter and Kelsey, 1991; Cronquist, 1994; McArthur, 1994). The subgenus can be considered as a large species complex (Clausen, 1951) centered on *A. tridentata* because hybridization between taxa (species and subspecies) is possible (McArthur et al., 1979). However, polyploidy in several taxa complicates gene exchange possibilities (Ward, 1953; Taylor, Marchand, and Crompton, 1964; McArthur, Pope, and Freeman, 1981). Evidence from different scientific discipline sources support *Tridentatae* as a cohesive, monophyletic group, i.e., internal transcribed spacer (ITS) sequences of nuclear ribosomal DNA, and chloroplast DNA restriction site data (Kornkven, 1997; Kornkven, Watson, and Estes, 1998, 1999; Torrell et al., in press), hybridization and karyotypic data (McArthur and Plummer, 1978; McArthur et al., 1979; McArthur, Pope, and Freeman, 1981), randomly amplified polymorphic DNA (RAPD) data (McArthur et al., 1998c), and flavonoid, terpenoid, and especially sesquiterpene lactone chemical data (Greger, 1978; Seaman, 1982; Jeffrey, 1995). Of the 11 *Tridentatae* species listed above only two have had their status within *Tridentatae* questioned: *Artemisia bigelovii* because its flower heads often include a ray flower within otherwise discoid heads (other *Tridentate* are uniformly discoid), and

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A. pygmaea, because of its resinous-glandular, 5–9 lobed leaves and diminutive stature. But the balance of evidence favors inclusion of these species within *Tridentatae* (McArthur et al., 1998b, and references therein).

Ling (1982, 1995), Weber (1984), and Bremer and Humphries (1993) have recognized *Seriphidium* (Besser) Fourr. at the generic level with inclusion of members of the *Tridentatae.* That proposal has not been generally accepted—only one of the numerous references to chromosome counts in *Index to Plant Chromosome Numbers* list *Seriphidium,* whereas 514 reference *Artemisia* (Goldblatt, 1981, 1984, 1985, 1988; Goldblatt and Johnson, 1990, 1991, 1994, 1996, 1998).

The *Tridentatae* have been important in Western North America since the Pliocene (McArthur, Pope, and Freeman, 1981; Thompson 1991). Two principal hypotheses are extant in regard to the origin of the *Tridentatae.* Ling (1991, 1995) and Bremer and Humphries (1993) suggest that the group originated from Eurasian *Seriphidium* species that migrated over the Bering Strait, whereas McArthur and associates (McArthur and Plummer, 1978; McArthur, Pope, and Freeman, 1981) suggest that the group evolved from herbaceous members of subgenus *Artemisia* in situ in North America and differentiated during the extreme climatic fluctuations of the Pleistocene. Subgenus *Artemisia* species are circumboreal but are centered on the great Eurasian landmass. Both hypotheses remain viable in face of the available molecular (Kornkven, 1997; Kornkven, Watson, and Estes, 1998), morphological, anatomical, karyotypical, and chemical data (Rydberg, 1916; Hall and Clements, 1923; Ward, 1953; Carlquist, 1966; Greger, 1978; McArthur and Plummer, 1978; Seaman, 1982; Shultz, 1983; Bremer and Humphries, 1993; Jeffrey, 1995; Ling, 1995).

The genus *Artemisia* has received extensive cytological study, e.g., *Index to Plant Chromosome Numbers* (nine volumes, 1975–1995, Goldblatt, 1981, 1984, 1985, 1988; Goldblatt and Johnson, 1990, 1991, 1994, 1996, 1998) lists 515 records (one as *Seriphidium*). The genus has two principal base chromosome numbers, $x = 8$ and $x = 9$. The *Index to Plant Chromosome Numbers* database shows $x = 9$ to be the dominant base number (85.6%) with $x = 8$ much smaller (9.7%) and with the balance consisting of aneuploids at the diploid or higher levels. Polyploidy, up to 12x, is common, but the vast majority of taxa are 2–6x (Keck, 1946; Ehrendorfer, 1964; Estes, 1969; Persson, 1974; McArthur and Pope, 1979; Stahevitch and Wojtas, 1988; Vallès Xirau and Siljak-Yakovlev, 1997). The subgenus *Tridentatae* ($x = 9$) has been the subject of two major (Ward, 1953; McArthur, Pope, and Freeman, 1981) and several smaller scope chromosome studies (Table 1). The current study was initiated to examine more fully *Tridentatae* cytogeography, especially the extent and nature of polyploidy (McArthur, Pope, and Freeman, 1981), the incidence of polyploidy within populations, and the interface of ploidy levels between adjacent populations. Although most of the chromosome number data were obtained specifically for this study, additional data collected to aid other research efforts are also included (McArthur and Welch, 1982; Van Epps, Barker, and McKell, 1982; Goodrich, McArthur, and Winward, 1985; McArthur and Goodrich, 1986; McArthur, Welch, and Sanderson, 1988; Scott, McCoy, and Wullstein, 1989; Fairchild, 1990; Freeman et al., 1991; Rosentreter and Kelsey, 1991; Welch et al., 1992; Downs, Soltis, and Black, 1995; Graham, Freeman, and McArthur, 1995; Johnson-Barnard, 1995; Pounds, 1997; Wang et al., 1997; Ayre, 1998; McArthur et al., 1998a, b, c; Freeman et al., 1999).

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

[a] Data from Keil and Pinkava (1979—one population), McArthur et al. (1981—120 populations) and references cited therein (124 populations), Barker and McKell (1986—six populations), Stahevitch and Wojtas (1988—two populations) and Table 2 (364 populations—excluding the hybrid populations). The count reported by Diettert (1938)—the first report for subgenus *Tridentatae*—is not included because he stated a count of $2n = 18$ but illustrated a count of $n = 18$ (Clausen, Keck, and Hiesey, 1940; Ward, 1953).

[b] Includes only subspecies for which chromosome numbers have been determined. There are additional subspecific taxa that are cytologically unknown: *A. arbuscula* ssp. *thermopola, A. nova* var. *duchesnicola,* and *A. tripartita* ssp. *rupicola* (Beetle, 1960; Welsh and Goodrich, 1995).

[c] Some populations have plants at more than one chromosome ploidy level—see McArthur et al. (1981) and Table 2. The ploidy (x) level reported here is that of the mode of the sampled population(s) or the lowest number when equal numbers of plants were at different x levels.

[d] The *A. arbuscula* 6x populations include two populations reported as *A. tridentata* ssp. *wyomingensis* in our earlier cytotaxonomic work of the *Tridentatae* (McArthur et al., 1981). Our M&S 1501 (Table 2) is a recollection of one of these populations. *Artemisia tridentata* ssp. *wyomingensis* is almost certainly exclusively 4x (Table 2), as Winward and McArthur (1995) reported: ''We . . . suspect both bona fide *A. tridentata* ssp. *wyomingensis* and *A. arbuscula* ssp. *longicaulis* were growing in the accessional rows.''

[e] We have accepted the narrow definition of *A. rothrockii,* i.e., a viscous polyploid of the Sierra Nevada and close outliers (Ward, 1953; Goodrich et al., 1985; McArthur and Goodrich, 1986; Shultz, 1986). Three populations (Swasey Ridge, Sanpete Co., Utah, *U*-1; Olsen Bench, Sanpete Co., Utah, *U*-2; and Blind Bull Creek, Lincoln Co., Wyoming, M–1149) treated as *A. rothrockii* in our earlier cytotaxonomic publication (McArthur et al., 1981) have been transferred to *A. tridentata* ssp. *spiciformis* in this table and in Figs. 4 and 6.

MATERIALS AND METHODS

Chromosome counts—Both meiotic and mitotic chromosome counts were made. Meiotic counts were used as the preferred technique, therefore avoiding the possibility of scoring endomitosis. However, when flower buds were not available mitotic counts were performed. For some populations both meiotic and mitotic counts were made. We usually made chromosome counts for several plants per population because an earlier study (McArthur, Pope, and Freeman, 1981) demonstrated that more than one ploidy level was present in some populations. Mitotic tissue was examined from root tips pretreated overnight in cold water (~3°C) and fixed in 5% aqueous acetic acid, hydrolyzed in 1 mol/L

TABLE 2. New chromosome counts in subgenus *Tridentatae* of *Artemisia*.

Taxa	Locality, collection number[a]	No. of plants sampled[b]	*n*	2*n*[c]
A. arbuscula Nutt. ssp. *arbuscula*	Ebbet's Pass, Alpine Co., California, M&S *s.n.*, 18 Aug. 1987, 2660 m	2	9	
	Ancient Bristlecone Forest, White Mountains, Inyo Co., California, M&S 2166, 3065 m	2 1	9 18	
	Gilbert Summit, Inyo Co., California, M&S 2164, 1920 m	3	18	
	Westgard Pass, White Mountains, Inyo Co., California, M&S 2165, 2230 m	2	18	
	Noble, Lassen Co., California, J. A. Young *s.n.*, 'low', December 5, 1989, 1525 m	5		36
	Noble, Lassen Co., California, J. A. Young *s.n.*, 'Lahontan', December 5, 1989, 1525 m	3		36
	Shaffer Mountains, Lassen Co., California, M&S 1591, 1340 m	2	18	
	8 km east of Ft. Bidwell, Modoc Co., California, M&S 1589, 1525 m	2	18	
	24 km north of Ft. Bidwell, Modoc Co., California, M&S 1588, 1615 m	2	18	
	Birch Springs Road, Mt. Borah, Custer Co., Idaho, M&S 2107B, 2010 m	3	18	
	May Road, north of Mt. Borah, Custer Co., Idaho, M&S *s.n.* 7 July 1992, 1585 m	1	18	
	Summit Creek, Little Lost River Valley, Custer Co., Idaho, M&S 2112, 2040 m	4	18	
	Lida, Esmeralda Co., Nevada, M&S 2137, 1880 m	4	18	
	11 km south of Lida, Esmeralda Co., Nevada, M&S 2386, 1740 m	4	18	
	2 km southeast of Palmetto, Esmeralda Co., Nevada, M&S 2138, 1920 m	3	18	
	6 km southeast of Palmetto, Esmeralda Co., Nevada, M&S 2163, 1860 m	2	18	
	Pinto Summit, 8 km south of Eureka, Eureka Co., Nevada, M&S 2171, 2250 m	3	9	
	Austin Summit, Lander Co., Nevada, M&S 2139, 2280 m	1	9	
	Buffalo Hills, Washoe Co., Nevada, M&S 1592, 1465 m	2	9	
	24 km south of Adel, Lake Co., Oregon, M&S 1587, 1665 m	2	9	
	16 km south of Plush, Lake Co., Oregon, M&S 1586, 1370 m	2	18	

TABLE 2. Continued.

Taxa	Locality, collection number[a]	No. of plants sampled[b]	*n*	2*n*[c]
	Goose Creek Mountains, Box Elder Co., Utah, M. M. Petersen 3, 2010 m	2		18
A. arbuscula Nutt. ssp. *longicaulis* Winward & McArthur	Topaz Lake, Douglas Co., Nevada, M&S 1594, 1585 m	1	27	
	Trout Creek Basin, Humbolt Co., Nevada, M&S 1501, 1340 m	15	27	
	Dayton, Lyon Co., Nevada, M&S 1595, 1355 m	1	27	
	Toulon, Pershing Co., Nevada, M&S 1593, 1355 m	2	27	
	Mustang, Washoe Co., Nevada, M&S 1684, 1220 m	2	27	
	Sutcliff Turnoff, Washoe Co., Nevada, M&S 1596, 1200 m	2	27	
	32 km east of Adel, Lake Co., Oregon, M&S 1590, 1365 m	2	27	
A. bigelovii Gray	Edge of Kaibab Plateau, 28 km southeast of Fredonia, Coconino Co., Arizona, M&S 2532, 1800 m	2	36	
	Sand Bench, 15 km east of Fremont Junction, Emery Co., Utah, M&S 2509, 1780 m	3	18	
A. cana Pursh. ssp. *cana*	Medicine Hat, Alberta, Canada, M&S 2489, 745 m	2	36	
	Patricia, Alberta, Canada, M&S 2488, 730 m	2	36	
	Coulee east of Turin, Alberta, Canada, M&S 2487, 855 m	2	36	
	8 km north of Wildhorse, Alberta, Canada, M&S 2486, 870 m	3	36	
	24 km south of Assiniboia, Saskatchewan, Canada, M&S 2491, 760 m	2	36	
	Piapot, Saskatchewan, Canada, M&S 2490, 755 m	3	36	
	Maybell, Moffat Co., Colorado, M&S 2120, 1830 m	1	36	
	8 km north of Great Falls, Cascade Co., Montana, M&S 2482, 1030 m	1	36	
	Ft. Benton, Chouteau Co., Montana, M&S 2483, 800 m	4	36	
	32 km east of Lewiston, Fergus Co., Montana, M&S 2113, 1130 m	3	36	
	Havre, Hill Co., Montana, M&S 2485, 760 m	2	36	
	Livingston, Park Co., Montana, M&S 2111, 1375 m	1	36	
	Poplar, Roosevelt Co., Montana, M&S 2494, 605 m	1	36	
	Plentywood, Sheridan Co., Montana, M&S 2495, 625 m	3	36	

TABLE 2. Continued.

Taxa	Locality, collection number[a]	No. of plants sampled[b]	*n*	2*n*[c]
	8 km east of Glasgow, Valley Co., Montana, M&S 2492, 635 m	1	36	
	13 km west of Fryburg, Billings Co., North Dakota, M&S 2498, 825 m	3	36	
	Watford City, McKenzie Co., North Dakota, M&S 2496, 640 m	2	36	
	Edgemont, Fall River Co., South Dakota, M&S 2117, 1055 m	1	36	
	3 km north of Upper Brule, Lyman Co., South Dakota, M&S 2500, 530 m	1	36	
	6 km east of Scenic, Pennington Co., South Dakota, M&S 2501, 840 m	2	36	
	Barlow Ranch southwest of Gillette, Campbell Co., Wyoming, G. P. Jones *s.n.* 1987, 1555 m	7		72
	Douglas, Converse Co., Wyoming, M&S 2118, 1470 m	2	36	
	16 km west of Alcova, Natrona Co., Wyoming, M&S 2127, 1920 m	1	36	
	Sheridan, Sheridan Co., Wyoming, M&S 2128, 1140 m	1	36	
A. cana Pursh. ssp. *viscidula* (Osterhout) Beetle	21 km east of Lakeview, Lake Co., Oregon, M&S 1582, 1705 m	2	18	
	Moon Lake, Duchesne Co., Utah, M&S 2129, 2475 m	2	9	
	Red Creek Hole, east of Wasatch Pass, Sevier Co., Utah, M&S 2152, 2305 m	3	9	
	Soldier Fork, west of Soldier Summit, Utah Co., Utah, M&S 2146, 2195 m	3	9	
	Soldier Summit, Wasatch Co., Utah, A. P. Plummer *s.n.* 1975, 2255 m	1	9	
A. nova Nelson	32 km east of Paradox, Montrose Co., Colorado, M&S 2512, 1645 m	2	18	
	Birch Springs Road, Mt. Borah, Custer Co., Idaho, M&S 2107A, 2,010 m	3	9	
	Mackay, Custer Co., Idaho, M&S *s.n.* 7 July 1992, 1795 m	1	9	
	Goldfield Summit, Esmeralda Co., Nevada, M&S 2161, 1855 m	1	18	
	Lida Summit, Esmeralda Co., Nevada, M&S 2162, 2225 m	3	9	
	Hickison Summit, Lander Co., Nevada, M&S 2169, 2000 m	1	18	
	15 km east of Panaca, Lincoln Co., Nevada, M&S 2156, 1830 m	1	18	

TABLE 2. Continued.

Taxa	Locality, collection number[a]	No. of plants sampled[b]	*n*	2*n*[c]
	45 km east of Tonopah, Nye Co., Nevada, M&S 2159, 1935 m	2	18	
	Warm Springs Summit, Nye Co., Nevada, M&S 2158, 1920 m	3	18	
	16 km south of Eureka, White Pine Co., Nevada, M&S *s.n.* 30 July 1993, 1870 m	1	18	
	East of Pancake Summit, Newark Valley, White Pine Co., Nevada, M&S 2173, 1890 m	1	18	
	34 km south of Burns Junction, Malheur, Oregon, M&S 2361, 1265 m	2	18	
	Pine Valley Ridge, 4 km north of Desert Experimental Range, Millard Co., Utah, B. L. Welch *s.n.* October 1992, 1820 m	2		36
	3 km southeast of Laramie, Albany Co., Wyoming, G. P. Jones 153, 2300 m	1		18
	16 km west of Medicine Bow, Carbon Co., Wyoming, G. P. Jones 134, 2165 m	2		18
A. pygmaea Gray	Along I-70, north of San Rafael Knob, San Rafael Swell, Emery Co., Utah, M&S 2510, 2195 m	3	9	
	Yuba Dam Road, 0.5 km south of Mills Exit, I-15, Juab Co., Utah, M&S 2508, 1535 m	3	9	
A. rigida (Nutt.) Gray	Malheur Reservoir, Malheur Co., Oregon, M&S *s.n.* 13 September 1994, 1035 m	3	9	
	Fitzner/Eberhardt Arid Lands Ecology Reserve, Hanford Site, Benton Co., Washington, J. L. Downs, *s.n.* 4 September 1994, 915 m	1	18	
	Umtanum Ridge Slope, Yakima Training Center, Yakima Co., Washington, M&S 2345, 855 m	1	18	
A. tridentata Nutt. ssp. *spiciformis* (Osterhout) Goodrich &McArthur	Cross Creek, Minturn, Eagle Co., Colorado, M&S 1428, 2440 m	2	9	
	Whitney Guard Station, Wasatch National Forest, Summit Co., Utah, S. Goodrich 19693, 2870 m	1	9	
	Wolf Creek Summit, Uinta National Forest, Wasatch Co., Utah, S. Goodrich 17515, 2870 m	1	9	
	Wolf Creek Pass, Uinta National Forest, Wasatch Co., Utah, McArthur & Goodrich 1652, *s.n.* 1981, 2860 m	2[d]		18

TABLE 2. Continued.

Taxa	Locality, collection number[a]	No. of plants sampled[b]	n	$2n$[c]
A. tridentata Nutt. ssp. *tridentata*	South of Fredonia, Coconino Co., Arizona, G. L. Jorgensen U-134, 1465 m	2		36
	8 km south of Ravendale, Lassen Co., California, M&S 2384, 1640 m	1	9	
	24 km north of Litchfield, Lassen Co., California, M&S 2385, 1350 m	3	9	
	Newell, Modoc Co., California, M&S 2378, 1230 m	1	9	
	Canby, Modoc Co., California, M&S 2380, 1315 m	1	9	
	8 km east of Canby, Modoc Co., California, M&S 2381, 1320 m	2	9	
	2 km south of Alturas, Modoc Co., California, M&S 2382, 1330 m	3	9	
	6 km south of Ventucopa, Los Padres National Forest, Ventura Co., California, M&S *s.n.* October 8, 1988, 990 m	1	18	
	12 km east of Dove Creek, Delores Co., Colorado, G. S. Van Epps & J. R. Barker 22 (U-115), 2025 m	3		18
	Disappointment Creek, San Juan National Forest, Delores Co., Colorado, G. A. Van Epps & J. R. Barker 6 (U-111), 1950 m	9		18
	10 km north of Cowdrey, Jackson Co., Colorado, McArthur U-108, 2440 m	6		18
	Dinosaur, Moffat Co., Colorado, McArthur & Jorgensen 1744 (U-137), 1785 m	2	9	
	8 km east of Bedrock, Montrose Co., Colorado, M&S 2513, 1585 m	1	18	
	3 km west of Meeker, Rio Blanco Co., Colorado, M&S 1371, 1880 m	1	9	
	11 km east of Meeker, Rio Blanco Co., Colorado, G. S. Van Epps & J. R. Barker 34 (U-119), 1965 m	4		18
	3 km south of Dinosaur, Rio Blanco Co., Colorado, M&S 1437, 1755 m	27	9	
	24 km southwest of Malta, Cassia Co., Idaho, M&S 2311, 1615 m	2	9	
	Birch Creek, Challis National Forest, Custer Co., Idaho, M&S *s.n.* July 27, 1992, 1645 m	1	9	
	Rio Grande Drainage, 2 km west of Mackay, Custer Co., Idaho, M&S 2100, 2075 m	2	9	
	Hammett, Elmore Co., Idaho, M&S 2390, 810 m	1	9	
	6 km north of Twin Falls, Jerome Co., Idaho, M&S 2391, 1120 m	2	9	
	Salmon, Lemhi Co., Idaho, M&S *s.n.* August 27, 1987, 1210 m	2	9	
	8 km northeast of Weiser, Washington Co., Idaho, M&S 2364, 760 m	3	9	
	Dell, Beaverhead Co., Montana, M&S *s.n.*, July 28, 1992, 1830 m	2	9	
	Eastgate, Churchill Co., Nevada, M&S 1464, 1560 m	2	9	
	10 km north of Wells, Elko Co., Nevada, G. A. Van Epps & J. R. Barker 24 (U-116), 1760 m	2	9	
	Palmetto, Esmeralda Co., Nevada, Van Epps & Barker 28 (U-117), 1890 m	5		18
	Dayton, Lyon Co., Nevada, S. E. Meyer 24 (U-149), 1335 m	2		18
	1 km west of Stagecoach, Lyon Co., Nevada, S. E. Meyer 21 (U-147), 1330 m	3		36
	Currant, Nye Co., Nevada, M&S 2388, 1885 m	3	9	
	Baker, White Pine Co., Nevada, M&S 1445, 1625 m	1	9	
	Ely, White Pine Co., Nevada, G. A. Van Epps & J. R. Barker 45 (U-120), 1960 m	3		18
	John Day River Canyon, 20 km north of Dayville, Grant Co., Oregon, M&S 2354, 670 m	4	9	
	20 km north of Burns, Harney Co., Oregon, M&S 2374, 1310 m	2	9	
	Willowdale, Jefferson Co., Oregon, M&S 2377, 550 m	3	9	
	8 km north of Harper, Malheur Co., Oregon, M&S 2321, 1160 m	3	9	
	29 km northeast of Ironside, Malheur Co., Oregon, M&S 2330, 1065 m	4	9	
	Kane Springs, Malheur Co., Oregon, M&S 2319, 945 m	3	9	
	Oregon Trail Monument, Captain Keeney Pass, Malheur Co., Oregon, M&S 2318, 885 m	3	9	
	Along Owyhee River, 24 km below Owyhee Reservoir, Malheur Co., Oregon, M&S 2315, 710 m	3	9	
	29 km northeast of Lexington, Morrow Co., Oregon, M&S 2348, 370 m	3	9	
	Ruggs, Morrow Co., Oregon, M&S 2349, 645 m	3	9	
	3 km east of Umatilla, Umatilla Co., Oregon, M&S 2332, 150 m	3	9	

TABLE 2. Continued.

Taxa	Locality, collection number[a]	No. of plants sampled[b]	*n*	2*n*[c]
	45 km south of Maupin, Wasco Co., Oregon, M&S 2376, 980 m	2	9	
	Bluff above Tygh Valley, Wasco Co., Oregon, M&S 2375, 490 m	3	9	
	5 km east of Spray, Wheeler Co., Oregon, M&S 2351, 550 m	3	9	
	10 km southeast of Snowville, Box Elder Co., Utah, M&S 2310, 1390 m	2	9	
	Gordon Creek Wildlife Management Area, 15 km west of Spring Glenn, Carbon Co., Utah, M&S 2180A, 1980 m	4		18
	Martin's Draw, Daggett Co., Utah, M&S 1599, 1990 m	2	9	
	Indian Canyon, Duchesne Co., Utah, McArthur U-122, 1980 m	3[d]		18
	Huntington Canyon, Emery Co., Utah, S. E. Meyer *s.n.* 1986 (U-040), 1950 m	3		36
	San Rafael Swell, Emery Co., Utah, G. A. Van Epps and J. R. Barker 29 (U-118), 2135 m	12		18
	Antimony, Garfield Co., Utah, G. A. Van Epps and J. R. Barker 16 (U-114), 1980 m	8		18
	Hatch, Garfield Co., Utah, G. L. Jorgensen U-031, 2110 m	2		18
	3 km south of Levan, Juab Co., Utah, G. L. Jorgensen U-132, 1610 m	3		18
	Tintic Valley, 8 km south of Eureka, Juab Co., Utah, M&S *s.n.* August 27, 1986, 1755 m	1	9	
	Salt Creek Canyon, 9 km east of Nephi, Juab Co., Utah, G. A. Van Epps and J. R. Barker 1 (U-109), 1770 m	4		18
	Nebo Loop Road, below Salt Cave Hollow, Salt Creek Canyon, 10 km east of Nephi, Juab Co., Utah, M&S 2503, 1780 m	5	9	
	Johnson Canyon, Kane Co., Utah, G. A. Van Epps and J. R. Barker 13 (U-121), 1735 m	5[d]		18
	Scipio Pass, Millard Co., Utah, M&S 1814, 1820 m	2	9	
	2 km south of Marysvale, Piute Co., Utah, G. L. Jorgensen U-133, 1815 m	2		18
	9 km north of Ephraim, Sanpete Co., Utah, G. L. Jorgensen U-011, 1700 m	1	9	

TABLE 2. Continued.

Taxa	Locality, collection number[a]	No. of plants sampled[b]	*n*	2*n*[c]
	Clear Creek Canyon, 3 km west of Sevier, Sevier Co., Utah, M&S 2089, *s.n.*, August 20, 1992 1735 m	2	9	
	1 km west of Narrows, Clear Creek Canyon, Sevier Co., Utah M&S *s.n.*, August 20, 1992, 1790 m	3	9	
	Canyon bottom, Clear Creek Canyon, 10 km west of Sevier, Sevier Co., Utah M&S 2088, *s.n.*, August 20, 1992, 1790 m	3	9	
	5 km east of Cove Fort Summit, Clear Creek Canyon, Sevier Co., Utah, M&S *s.n.*, August 25, 1994, 2035 m	4	9	
	2 km west of Boulter Canyon, Tooele Co., Utah, M&S *s.n.* August 27, 1985, 1830 m	2		36
	18 km southeast of Jensen, Uintah Co., Utah, M&S *s.n.* 1985, 1585 m	1	9	
	1 km north of Maeser, Uintah Co., Utah, G. A. Van Epps & J. R. Barker 4 (U-110), 1740 m	7		18
	Diamond Fork Canyon, Utah Co., Utah, M&S 1386, 1555 m	2	9	
	Mouth of Spanish Fork Canyon, Utah Co., Utah, M&S *s.n.*, September 15, 1986, 1480 m	1	9	
	4 km west of Francis, Wasatch Co., Utah, S. E. Meyer 14 (U-140), 1905 m	3		18
	6 km south of Pinto, Washington Co., Utah, M&S 2179, 1920 m	3	9	
	Horn Rapids Dam, Yakima River Flood Plain, Benton Co., Washington, M&S 2336, 130 m	5	9	
	Sun Lakes, 8 km southwest of Coulee City, Grant Co., Washington, M&S 2366, 380 m	2	18	
	Malot, Okanogan Co., Washington, M&S 2368, 255 m	3	18	
	2 km south of Oroville, Okanogan Co., Washington, M&S 2369, 90 m	3	18	
	2 km west of Oroville, Okanogan Co., Washington, M&S 2370, 105 m	4	18	
	2 km north of Medicine Bow, Carbon Co., Wyoming, G. P. Jones 127, 2010 m	1		18

TABLE 2. Continued.

Taxa	Locality, collection number[a]	No. of plants sampled[b]	n	$2n$[c]
	15 km northwest of Medicine Bow, Carbon Co., Wyoming, G. P. Jones 130, 2040 m	5		18
	3 km north of Kemmerer, Lincoln Co., Wyoming, McArthur & Jorgensen 1736 (U-106), 2135 m	3		18
	Cody, Park Co., Wyoming, G. A. Van Epps & J. R. Barker 10 (U-112), 1530 m	4		18
	Daniel, Sublette Co., Wyoming, M&S 1741 (U-135), 2190 m	2		18
	Base of North Table Mountain, 45 km northeast of Rock Springs, Wyoming, M&S 1577, 2225 m	5	9	
	Patrick Draw, Sweetwater Co., Wyoming, M&S 1571, 2055 m	2	9	
	Rock Springs, Sweetwater Co., Wyoming, G. A. Van Epps & J. R. Barker 11 (U-113), 1910 m	4	9	
	16 km south of Elkol, Uinta Co., Wyoming, M&S *s.n.* 1984, 2030 m	2		18
	Albert Creek, 20 km north of Evanston, Uinta Co., Wyoming, M&S 1735, 2040 m	2		18
A. tridentata Nutt. ssp. *vaseyana* (Rydb.) Beetle	65 km southeast of Ensenada, Baja California, Mexico, M&S 2199, 600 m	2		36
	10 km northwest of Jacob's Lake, Coconino Co., Arizona, G. L. Jorgensen U-071, 2100 m	2		18
	Tejon Pass, Kern Co., California, M&S 2200, 1270 m	3		36
	Sage Hen Summit, north of Madelin, Lassen Co., California, M&S *s.n.*, August 17, 1994, 1620 m	3	18	
	North of Lookout, northwest corner of Big Valley, Modoc Co., California, M&S 2379, 1275 m	2	18	
	24 km north of Ft. Bidwell, at state line, Modoc Co., California, M&S 1585, 1625 m	1	18	
	16 km west of Jacumba, San Diego Co., California, M&S 2198, 610 m	3		36
	Minturn, Eagle Co., Colorado, M&S 1427, 2400 m	1	9	
	Walden, Jackson Co., Colorado, McArthur & Jorgensen U-061, 2470 m	5 2[d]		18 36
	Poncha Pass, Saguache Co., Colorado, M&S 2122, 2475 m	3	9	
	Rio Grande Drainage, 7 km west of Mackay, Custer Co., Idaho, M&S 2101, 2315 m	8	9	
	16 km east of Mountain Home, Elmore Co., Idaho, M&S *s.n.*, August 1987, 1465 m	2	18	
	16 km east of Bozeman, Gallatin Co., Montana, M&S *s.n.*, July 28, 1992, 1570 m	2	9	
	16 km north of Helena, Lewis and Clark Co., Montana, M&S 2481, 1300 m	3	18	
	Pinto Summit, Eureka Co., Nevada, M&S 2172, 2220 m	3	9	
	Lida Summit, Esmeralda Co., Nevada, M&S 2140, 2260 m	5	18	
	Austin Summit, Lander Co., Nevada, M&S 2167, 2280 m	3	9	
	Coyote Summit, Lincoln Co., Nevada, M&S 2157, 2215 m	1	18	
	Currant Summit, Nye Co., Nevada, M&S 2389, 2215 m	2	9	
	Conner's Pass, White Pine Co., Nevada, M&S 1448, 2356 m	1	18	
	Robinson Summit, White Pine Co., Nevada, M&S 2175, 2300 m	2	18	
	Dooley Mountain Summit, Baker Co., Oregon, M&S 2331, 1665 m	3	9	
	Seneca, Grant Co., Oregon, M&S 2357, 1420 m	2	9	
	16 km east of Buchanon, Harney Co., Oregon, M&S 1583, 1450 m	2	18	
	Headquarters, Hart Mountain Refuge, Lake Co., Oregon, M&S 1584, 1710 m	2	9	
	13 km north of Westfall, Malheur Co., Oregon, M&S 2326, 1035 m	2	18	
	Above Clover Creek, 24 km northwest of Westfall, Malheur Co., Oregon, M&S 2328, 1205 m	2 1	9 18	
	Cottonwood Range, 39 km north of Westfall, Malheur Co., Oregon, M&S 2329A, 1465 m	2	9	
	Indian Peaks, Beaver Co., Utah, Jorgensen U-013, 2255 m	1	9	
	Sardine Canyon, Box Elder Co., Utah, B. L. Welch *s.n.* 1982, 1785 m	3[d]		18

TABLE 2. Continued.

Taxa	Locality, collection number[a]	No. of plants sampled[b]	n	$2n$[c]
	Head of Martin's Draw, Daggett Co., Utah, M&S 1597, 2105 m	1 1	9 18	
	Moon Lake, Duchesne Co., Utah, M&S *s.n.* 1982, 2480 m	1	9	
	Hatch, Garfield Co., Utah, Jorgensen U-070, 2120 m	2	9	
	Mud Spring Draw, Garfield Co., Utah, Jorgensen U-067, 2345 m	1	9	
	Nash Wash, Grand Co., Utah, M&S 2038, 1675 m	10	9	
	Bear Valley Summit, Iron Co., Utah, M&S *s.n.* 1984, 2410 m	6[d]		18
	Salt Cave Hollow, Salt Creek Canyon, Juab Co., Utah, M&S 2507, 1870 m	5	9	
	2 km southeast of Cove Fort, Millard Co., Utah, M&S *s.n.* August 24, 1984, 1860 m	4 1	9 	 18
	1 km north of Cove Fort, Millard Co., Utah, M&S *s.n.* August 24, 1984, 1800 m	1 1 1	9 18	 18
	2 km above Adelaide Campground, Corn Creek, Millard Co., Utah, M&S 1669, 1770 m	4	9	
	24 km west of Junction, Piute Co., Utah, M&S *s.n.* Augsut 28, 1992, 2470 m	2	9	
	Cove Fort Summit, Sevier Co., Utah, M&S 1488, 2155 m	2	9	
	Head of Clear Creek Canyon, east of Cove Fort Summit, Sevier Co., Utah, M&S 2085, 2075 m	8	9	
	2 km east of Cove Fort Summit, Clear Creek Canyon, Sevier Co., Utah, B. L. Welch, *s.n.* 1982, 1830 m	5 1		18 54
	7 km east of Salina Canyon Summit, Sevier Co., Utah, M&S 2148, 2135 m	2	18	
	4 km east of Salina Canyon Summit, Red Creek, Sevier Co., Utah, M&S 2149, 2305 m	3	9	
	House Park, Red Creek, Sevier Co., Utah, M&S 2151, 2410 m	6	9	
	Emigrant Pass, Salina Canyon Summit, Sevier Co., Utah, M&S 2150, 2400 m	5 2	9 18	
	Emigrant Pass, Salina Canyon Summit, Sevier Co., Utah, B. L. Welch, *s.n.* 1982, 2400 m	5		36
	Red Creek Hole, east of Salina Canyon Summit, Sevier Co., Utah, M&S 2153, 2305 m	2	9	
	3 km north of the mouth of Diamond Fork Canyon, Utah Co., Utah, M&S *s.n.* October 21, 1987, 1665 m	10 2[d] 1	9 	 18 36
	6 km east of the mouth of the Right Fork of Hobble Creek, Right Fork Hobble Creek Canyon, Utah Co., Utah, M&S *s.n.* 1985, 1720 m	8 9 3[d]	9 	 18 36
	4 km east of the mouth of the Right Fork of Hobble Creek, Right Fork Hobble Creek Canyon, Utah Co., Utah, M&S 1476, 2144, 2363, 1650 m	10 1	9 18	
	Mouth of Hobble Creek Canyon, Utah Co., Utah, McArthur & Plummer U-001, October 3, 1985, Goodrich, Winward, McArthur, and Lewis 21492, 1555 m	13	9	
	Mouth of Spanish Fork Canyon, Utah Co., M&S *s.n.* September 15, 1986, 1495 m	2	18	
	Near head of Soldier Fork, Utah Co., Utah, M&S 2131, 2195 m	4	9	
	Kyune Pass Road at U.S. 6, Price River, Utah Co., Utah, M&S 2135, 2190 m	1	18	
	Colton, Utah Co., Utah, M&S 2133, 2190 m	1	18	
	Spring Canyon, south of Colton, Utah Co., Utah, M&S 2134, 2345 m	4	9	
	Deer Creek Reservoir, Wasatch Co., Utah, M&S *s.n.* July 23, 1992, 1705 m	2	18	
	Soldier Summit, Wasatch Co., Utah, M&S 2132, 2195 m	2	9	
	Pine Valley, Washington Co., Utah, M&S 2177, 2010 m	3	9	
	Tabernacle Dome, Kolob Terrace, Washington Co., Utah, M&S 1821A, 1710 m	2	9	
	Utah Hill Summit, 24 km west of Santa Clara, Washington Co., Utah, M&S 2190, 1400 m	2	9	
	3 km south of forks of Pinto Canyon in South Fork, Pinto Canyon, Washington Co., Utah, M&S 2438, 2025 m	16 2	9 18	
	0.6 km south of forks of Pinto Canyon in South Fork, Pinto Canyon, Washington Co., Utah, M&S 2439, 1950 m	7 5	9 18	
	24 km north of Toquerville, Washington Co., Utah, M&S 2192, 4300 m	3	9	

TABLE 2. Continued.

Taxa	Locality, collection number[a]	No. of plants sampled[b]	n	$2n$[c]
	Diamond Valley Junction, northeast of Snows Canyon, Washington Co., Utah, M&S 2440, 1390 m	1 9	9 18	
	4 km north of Virgin, Washington Co., Utah, M&S 2191, 1125 m	6	18	
	8 km north of St. George, east of Snow Canyon, Washington Co., Utah, M&S 2189, 1340 m	5	18	
	16 km south of Kettle Falls, near Rice, Stevens Co., Washington, M&S 2371, 580 m	2	18	
	8 km north of Davenport, Lincoln Co., Washington, M&S 2372, 760 m	5	18	
	3 km north of Kemmerer, Lincoln Co., Wyoming, M&S 1737, 2135 m	2	9	
	2.5 km north of Daniel, Sublette Co., Wyoming, M&S 1742, 2195 m	3	9	
	Near Kelly, Teton Co., Wyoming, M&S 1536, 2075 m	2	9	
Artemisia tridentata Nutt. ssp. *wyomingensis* Beetle & Young	14 km southeast of Fredonia, Cocconino Co., Arizona, G. L. Jorgensen U-032, 1470 m	2		36
	Owen's Valley, Inyo Co., California, R. A. Woodward 301, 303, 305, 307, 1230 m	4	18	
	Noble, Lassen Co., California, J. A. Young *s.n.*, 'upland', December 5, 1989, 1525 m	3		36
	2 km north of Likely, Modoc Co., California, M&S 2383, 1340 m	1	18	
	8 km east of Ft. Garland, Costilla Co., Colorado, M&S 2124, 2530 m	3		36
	South-facing slope, near Blue Mesa Reservoir Bridge, Gunnison Co., Colorado, M&S 2517, 2220 m	2	18	
	Gunnison Basin, Gunnison Co., Colorado, J. Happ *s.n.* August 1986, 2360 m	2	18	
	Near State line, north of Walden, Jackson Co., Colorado, McArthur & Jorgensen U-011, 2560 m	2		36
	Cerro Summit, 16 km east of Montrose, Montrose Co., Colorado, M&S 2516, 2420 m	2	18	
	Ridgeway, Ouray Co., Colorado, M&S 2515, 2135 m	3	18	
	3 km south of Dinosaur, Rio Blanco Co., Colorado, M&S 1438, 1755 m	14	18	
	Birch Springs road, Mt. Borah, Custer Co., Idaho, M&S 2105, 1992, 1995 m	3	18	
	Challis, Custer Co., Idaho, B. L. Welch U-027, 1610 m	1		36
	Rio Grande drainage, 4 km west of Mackay, Custer Co., Idaho, M&S 2098, *s.n.*, July 27, 1992, 2135 m	2	18	
	Rio Grande drainage, 5 km west of Mackay, Custer Co., Idaho, M&S *s.n.*, July 27, 1992, 2165 m	3	18	
	Glenn's Ferry, Elmore Co., Idaho, B. L. Welch U-025, 785 m	2		36
	Salmon, Lemhi Co., Idaho, M&S *s.n.* August 27, 1987, 1220 m	2	18	
	1 km east of Warren, Carbon Co., Montana, M&S 1743, 1410 m	2		36
	Ft. Benton, Chouteau Co., Montana, M&S 2484, 800 m	1	18	
	32 km east of Lewiston, Fergus Co., Montana, M&S 2114, 1130 m	1	18	
	8 km east of Glasgow, Valley Co., Montana, M&S 2493, 635 m	2	18	
	Summit, south of Middlegate, Churchill Co., Nevada, M&S 1463, 1405 m	1	18	
	Oasis, Elko Co., Nevada, McArthur & Jorgensen U-026, 1800 m	2		36
	Beowawe Rest Stop, Eureka Co., Nevada, M&S *s.n.* 1984, 1525 m	2		36
	Monitor Valley, 8 km east of Hickison Summit, Lander Co., Nevada, M&S 2170, 1920 m	1	18	
	Scott Summit, Lander Co., Nevada, M&S 2168, 2370 m	3	18	
	Calavada Summit, 32 km south of Gabbs, Mineral Co., Nevada, M&S 1462, 1905 m	1	18	
	24 km west of Warm Springs, Nye Co., Nevada, M&S 1459, 1875 m	1	18	
	32 km southwest of Winnemucca, Pershing Co., Nevada, M&S *s.n.* 1984, 1305 m	3		36
	32 km south of Ely, White Pine Co., Nevada, M&S 1449, 2040 m	1	18	
	Baker, White Pine Co., Nevada, M&S 1444, 1630 m	1	18	
	Ely, White Pine Co., Nevada, McArthur U-012, 1960 m	1		36
	Jake's Valley, 48 km west of Ely, White Pine Co., Nevada, M&S 2174, 1980 m	1	18	

TABLE 2. Continued.

Taxa	Locality, collection number[a]	No. of plants sampled[b]	*n*	2*n*[c]
	Murray Summit, White Pine Co., Nevada, M&S 2387, 2230 m	3	18	
	Near Creek, east of Costilla, Taos Co., New Mexico, M&S 2519, 2395 m	3	18	
	On hillside, Costilla, Taos Co., New Mexico, M&S 2520, 2410 m	3	18	
	16 km southeast of Costilla, Taos Co., New Mexico, M&S 2521, 2530 m	3	18	
	16 km south of Taos, Taos Co., New Mexico, M&S 2522, 2180 m	2	18	
	13 km west of Fryburg, Billings Co., North Dakota, M&S 2499, 825 m	1	18	
	16 km west of Grassy Butte, McKenzie Co., North Dakota, M&S 2497, 810 m	5	18	
	Burns, Harney Co., Oregon, M. R. Haferkamp U-034, 1265 m	2		36
	2 km south of Narrows, Harney Co., Oregon, M&S 1581, 1250 m	2	18	
	24 km north of Westfall, Malheur Co., Oregon, M&S 2327, 1100 m	2	18	
	Hillside, 25 km north of Owyhee Reservoir, Malheur Co., Oregon, M&S 2316, 730 m	2	18	
	Hillside, Captain Keeney Pass, Malheur Co., Oregon, M&S 2317, 890 m	3	18	
	Hillside, 8 km north of Harper, Malheur Co., Oregon, M&S 2322, 870 m	5	18	
	Kane Springs, Malheur Co., Oregon, M&S 2320, 950 m	4	18	
	Cottonwood Range, 39 km north of Westfall, Malheur Co., Oregon, M&S 2329B, 1465 m	1	18	
	Gordon Creek, 7 km west of Spring Glenn, Carbon Co., Utah, M&S 2180B, 1980 m	4		36
	Gordon Creek, 8 km west of Spring Glenn, Carbon Co., Utah, B. L. Welch U-019, 1985 m	2		36
	Martin's Draw, Daggett Co., Utah, M&S 1603, 1990 m	3	18	
	Below Martin's Draw, Daggett Co., Utah, M&S 1604, 1980 m	4	18	
	Brown's Park, Daggett Co., Utah, B. L. Welch U-024, 1690 m	2		36
	Brown's Park, Daggett Co., Utah, M&S 1600, 1675 m	8	18	

TABLE 2. Continued.

Taxa	Locality, collection number[a]	No. of plants sampled[b]	*n*	2*n*[c]
	12 km south of Levan, Juab Co., Utah, G. L. Jorgensen U-022, 1605 m	2		36
	Tintic Pastures, Tintic Valley, Juab Co., Utah, K. K. Ayre *s.n.* September 4, 1996, 1690 m	6	18	
	Nash Wash, Grand Co., Utah, M&S 2036 1990, 1675 m	1	18	
	Cove Fort, Millard Co., Utah, M&S *s.n.* August 24, 1984, M&S 1484, 1830 m	14	18	
	3 km northwest of Cove Fort, Millard Co., Utah, M&S *s.n.* August 24, 1984, 1825 m	1	18	
	1 km west of Scipio, Millard Co., Utah, M&S *s.n.* 1987, 1615 m	2	18	
	Greenwich, Piute Co., Utah, M&S 1487, 2090 m	1	18	
	24 km west of Junction, Piute Co., Utah, M&S *s.n.* August 28, 1992, 2410 m	1	18	
	Near Piute Reservoir Dam, Piute Co., Utah, G. L. Jorgensen U-023, 1830 m	1		36
	Mayfield, Sanpete Co., Utah, M&S *s.n.* 1984, 1705 m	2		36
	Clear Creek Canyon, 1 km east of the Narrows, Sevier Co., Utah M&S *s.n.*, August 20, 1992, 1790 m	1	18	
	Hillside, Clear Creek Canyon, 10 km west of Sevier, Sevier Co., Utah M&S 2087, *s.n.*, August 20, 1992, 1785 m	5	18	
	Long Valley, Clear Creek Canyon, Sevier Co., Utah, M&S 2086, *s.n.*, August 28, 1994, 2105 m	4	18	
	5 km east of Cove Fort Summit, Clear Creek Canyon, Sevier Co., Utah, M&S *s.n.* August 29, 1992, August 25, 1994, 2035 m	8	18	
	Near Boulter Springs, 10 km southeast of Lofgreen, Tooele Co., Utah, M&S *s.n.* August 27, 1985, 1800 m	3	18	
	Rush Valley, 8 km south west of Mercur, Tooele Co., Utah, M&S *s.n.* August 1984, 1645 m	1	18	
	2 km west of Five Mile Pass, Rush Valley, Tooele Co., Utah, B. L. Welch U-021, 1600 m	2		36
	Diamond Fork Canyon, M&S 1386, Utah Co., Utah, 1555 m	3	18	

TABLE 2. Continued.

Taxa	Locality, collection number[a]	No. of plants sampled[b]	*n*	2*n*[c]
	Mouth of Spanish Fork Canyon, Utah Co., Utah, M&S *s.n.* September 15, 1986, 1495 m	2	18	
	Loa, Wayne Co., Utah, B. L. Welch U-020, 2140 m	3		36
	2 km below summit, Bobcat Canyon, Fitzner-Eberhart Arid Lands Ecology Reserve, Hanford Site, Benton Co., Washington, M&S 2341, 800 m	1	18	
	Base of Gable Mountain, Hanford Site, Benton Co., Washington, M&S 2334, 250 m	1	18	
	L. T. Murray Wildlife Preserve, Hanford Site, Yakima Co., Washington, J. L. Downs *s.n.* September 4, 1994, 1000 m	4	18	
	Hanford Site, Benton Co., Washington, M&S 2333, 250 m	1	18	
	Weather station, Fitzner/Eberhart Arid Lands Ecology Reserve, Hanford Site, Benton Co., Washington, M&S 2342, 400 m	2	18	
	Hillside, 8 km northwest of Coulee City, Douglas Co., Washington, M&S 2367, 535 m	3	18	
	8 km east of Ephrata, Grant Co., Washington, M&S 2365, 370 m	3	18	
	Hanson Creek Drainage, Saddle Mountains, Yakima Training Center, Kittitas Co., Washington, M&S 2346, 535 m	3	18	
	East side of Odessa, Lincoln Co., Washington, M&S 2373, 480 m	3	18	
	Range 25, Yakima Training Center, Yakima Co., Washington, M&S 2343, M. A. Pounds, *s.n.* 1991, 720 m	2 7	18	 36
	Umtanum Ridge slope, Yakima Training Center, Yakima Co., Washington, M&S 2344, 880 m	2	18	
	Taylor Pond, Yakima Training Center, Yakima Co., Washington, M. A. Pounds, *s.n.* 1991, 640 m	7		36
	LCTA plot 20, Yakima Training Center, Yakima Co., Washington, M. A. Pounds, *s.n.* 1991, 700 m	4		36
	3 km southwest of Bosler, Albany Co., Wyoming, G. P. Jones 105, 108, 109, 1545 m	3		36
	13 km north of Rock River, Albany Co., Wyoming, G. P. Jones 117, 2120 m	1		36
	2 km north of Medicine Bow, Carbon Co., Wyoming, G. P. Jones 127, 128, 2010 m	2		36
	Barlow Ranch southwest of Gillette, Campbell Co., Wyoming, G. P. Jones *s.n.* 1987, 1435 m	7		36
	6 km north of Kemmerer, Lincoln Co., Wyoming, M&S 1738 (U-028), 2135 m	2		36
	30 km northeast of Kemmerer, Lincoln Co., Wyoming, M&S 1739 (U-029), 2090 m	2		36
	2 km south of Daniel, Sublette Co., Wyoming, M&S 1740 (U-030), 2195 m	2		36
	Daniel, Sublette Co., Wyoming, M&S *s.n.* July 31, 1985, 2190 m	1		36
	1 km east of Daniel Junction, Sublette Co., Wyoming, M&S *s.n.* July 31, 1985, 2205 m	1		36
	Pinedale, Sublette Co., Wyoming, A. P. Plummer U-002, 2185 m	10[d]		36
	Boar's Tusk, 25 km southeast of Farson, Sweetwater Co., Wyoming, J. Johnson-Barnard 10, 31, 2165 m	2	18	
	Farson, Sweetwater Co., Wyoming, J. Johnson-Barnard 4, 9, 22, 27, 2000 m	4	18	
	Base of North Table Mountain, 45 km northeast of Rock Springs, Wyoming, M&S 1576, 2225 m	5	18	
	Patrick Draw, near Bitter Creek, Sweetwater Co., Wyoming, M&S 1570, 1575, 2060 m	11	18	
	Black Mountain, Sweetwater Co., Wyoming, J. Johnson-Barnard 1, 5, 25, 29, 2260 m	4	18	
	Cedar Mountain, Sweetwater Co., Wyoming, J. Johnson-Barnard 7, 18, 24, 2350 m	3	18	
	Cumberland, Uinta Co., Wyoming, J. Johnson-Barnard 2, 14, 16, 17, 2040 m	4	18	
	27 km south of Kemmerer, Uinta Co., Wyoming, M&S *s.n.* 1984, 2025 m	3		36
	8 km east of Newcastle, Weston Co., Wyoming, M&S 2502, 1330 m	2	18	
Artemisia tridentata Nutt. ssp. *xericensis* Winward	Mann Creek Reservoir, Washington Co., Idaho, M&S 2313, 915 m	2	18	

TABLE 2. Continued.

Taxa	Locality, collection number[a]	No. of plants sampled[b]	n	$2n$[c]
	2 km west of Mann Creek Reservoir, Washington Co., Idaho, M&S 2314, 945 m	4	18	
Artemisia tripartita Rydb. ssp. *tripartita*	Coalmont, Jackson Co., Colorado, A. P. Plummer U-001, 2500 m	1[d]		36
	Summit, Little Lost River Valley, Butte Co., Idaho, M&S July 27, 1992, 2050 m	3	9	
	Paddock 31, U.S. Sheep Station, Dubois, Clark Co., Idaho, M&S *s.n.* August 1994, 1675 m	2	18	
	West entrance, U.S. Sheep Station, Dubois, Clark Co., Idaho, M&S 2082, 2660 m	3	18	
	Birch Springs Road, Mt. Borah, Custer Co., Idaho, M&S *s.n.* July 27, 1992, 2020 m	3	9	
	Willow Creek Summit, Lemhi Co., Idaho, M&S *s.n.* August 21, 1987, 2225 m	2	9	
	Bobcat Canyon Summit, Fitzner/Eberhardt Arid Lands Ecology Reserve, Benton Co., Washington, M&S 2337, 900 m	1	9	
	2 km below summit, Bobcat Canyon, Fitzner/Eberhardt Arid Lands Ecology Reserve, Benton Co., Washington, M&S *s.n.* August 31, 1994, 800 m	1	9	
	Saddle Mountain, Hanson Creek Drainage, Yakima Firing Range, Kittitas Co., Washington, M&S 2347, 850 m	3	9	
Hybrid taxa				
A. cana Pursh. ssp. *cana* × *A. tridentata* Nutt. ssp. *wyomingensis* Beetle and Young (controlled hybridization)	M&S 2128 × M&S 1738	2	27	
A. tridentata Nutt. ssp. *tridentata* × *A. tridentata* Nutt. ssp. *vaseyana* (Rydb.) Beetle hybrid zone	Near Salt Cave Hollow, Salt Creek Canyon, Juab Co., Utah, M&S 2504, 2505, 2506, 1805 m	8 2	9 18	

[a] Collection numbers are presented as assigned by collectors, *s.n.* = no number assigned by collector, collection numbers starting with U are seed accession numbers, i.e., collections have been maintained via stored seed.

[b] Number of individual plants by chromosome number for which chromosome counts were made per population.

[c] n = gametic count from pollen mother cells; $2n$ = somatic count from root tips of germinating seedlings.

[d] b chromosomes present in at least some plants.

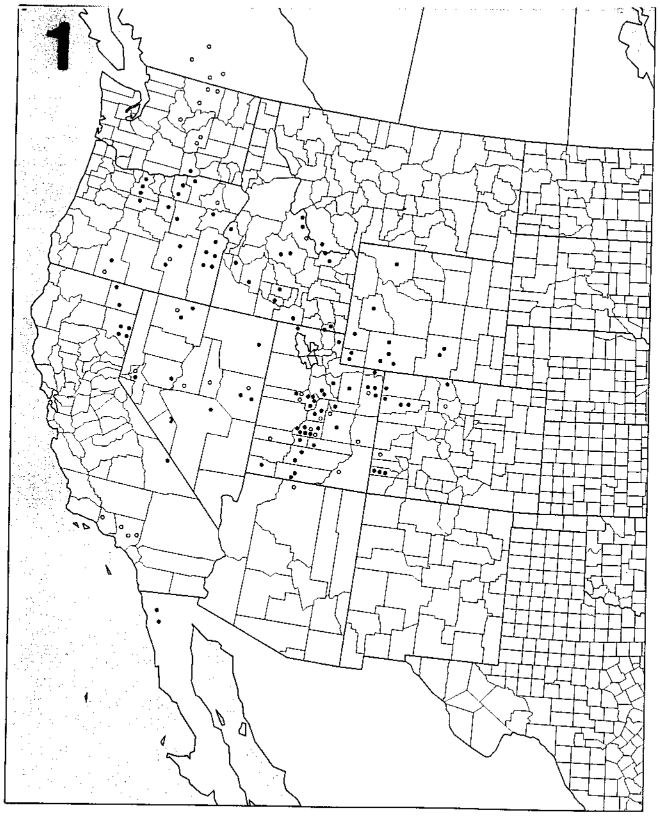
HCl for 5 h at room temperature (~20°C), stained in acetocarmine, and squashed in a drop of corn syrup. Meiotic material (pollen mother cells) was obtained from the field on appropriate dates, during August or early September. Flowering times of plants growing at higher altitudes and latitudes are generally earlier than those growing at lower altitudes and latitudes. Because of high reactivity of phenolics in sagebrush tissue, the customary use of acidic fixatives was replaced by the dehydrating solvents methanol or acetone (usually methanol) in order to obtain clear chromosomal preparations. Buds were collected in 100% methanol (or acetone) and kept up to 1.5 yr in refrigeration (~3°C), and pollen mother cells were squashed in acetocarmine for examination. Meiotic and mitotic slide preparations were made semipermanent by replacing the stain sequentially by 45% acetic acid and then corn syrup. Representative voucher specimens were collected and deposited in the Shrub Sciences Laboratory Herbarium (SSLP), some duplicates are also deposited in other herbaria (BRY, ID, MO, NY, OGDF, RENO, RM, UC, UT, UTC) (Holmgren, Holmgren, and Barnett, 1990).

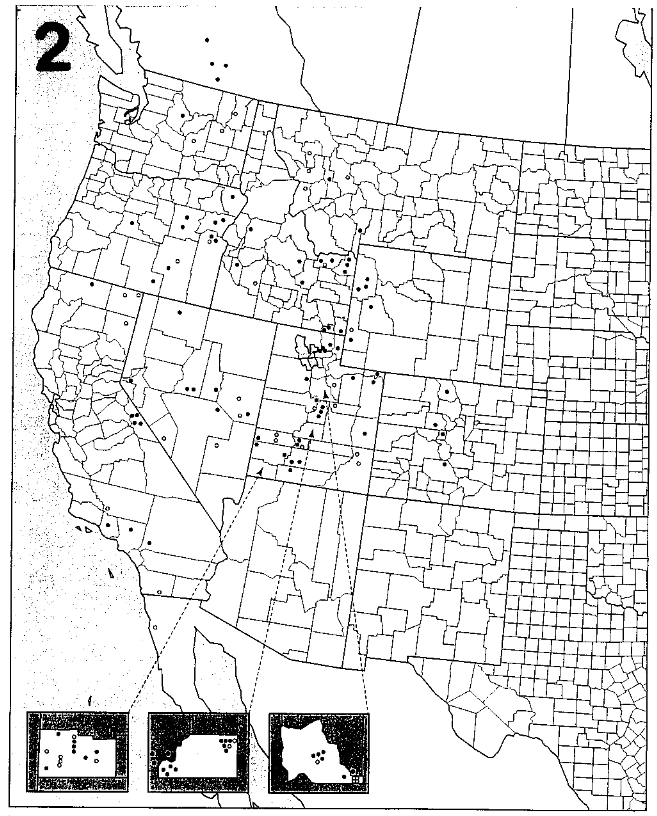
Plant identification—As we collected buds and worked with populations of *Tridentatae* taxa we used the taxonomic keys of Beetle (1960), McArthur (1983), Shultz (1986), and Cronquist (1994) with fine tuning of newly recognized taxa from Goodrich, McArthur, and Winward (1985), Rosentreter and Kelsey (1991), and Winward and McArthur (1995). Identification of *A. tridentata* ssp. *vaseyana* was confirmed by subjecting leaves or fixed bud solutions to a long-wave (364 nm) ultraviolet light test (Winward and Tisdale, 1969; Stevens and McArthur, 1974; McArthur, Pope, and Freeman, 1981). This taxon, in contrast to ssp. *tridentata* and ssp. *wyomingensis,* contains substantial concentrations of coumarin glycosides that are water and methanol soluble. These water and methanol solutions glow a bright iridescent blue color under an ultraviolet light. For many populations we scored the intensity of these compounds on a 0–5 scale, where 0 = no color and 5 = bright, blue color.

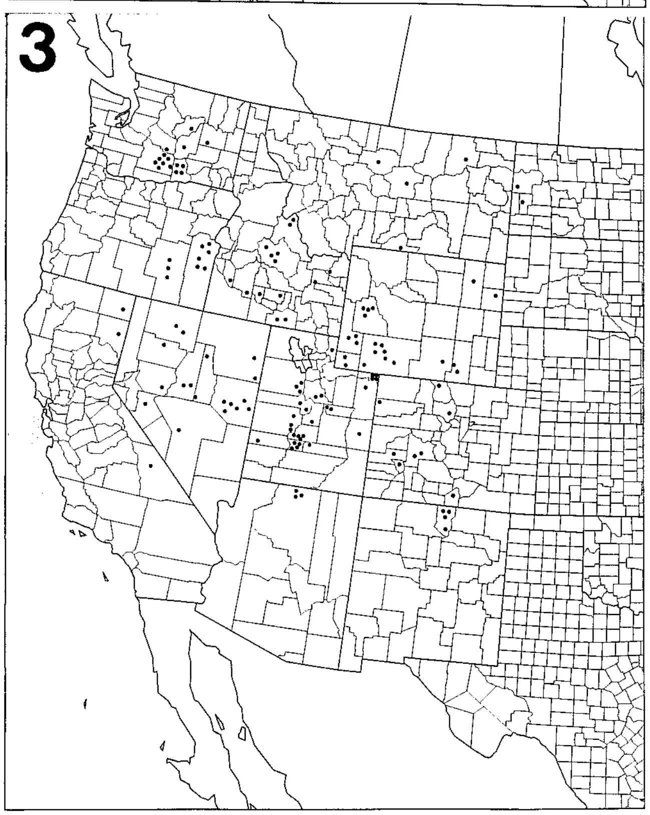
Measurements and analyses—Plants of several of the taxa have relative size differences even when growing in uniform gardens or in mixed stands (Beetle and Young, 1965; Marchand, McLean, and Tisdale, 1966; Winward and Tisdale, 1977; McArthur and Welch, 1982, Barker and McKell, 1986; Shumar and Anderson, 1986). We collected maximum height and crown diameter data (in centimetres) from individual mature plants from several populations where taxa co-occurred. Population means and comparisons between populations for height and crown were obtained using Proc Means and Proc GLM procedures of SAS statistical packages (SAS, 1989). *T* tests were used to compare the color intensity values of ultraviolet visible coumarin glycosides (Woolf, 1968). We accepted significant differences between means when $P < 0.05$.

RESULTS

Chromosome counts—Our chromosome counts are summarized in Table 1 with all other known counts for subgenus *Tridentatae* of *Artemisia.* Chromosome counts reported as a result of our current study are listed in Table 2. The counts there constitute ~60% of all counts that have been made (Figs. 1–6); adding those counts to those reported in McArthur, Pope, and Freeman (1981) the cumulative contribution from our laboratory is nearly 80% of total *Tridentatae* counts. First records are presented here: for *A. arbuscua* ssp. *longicaulis,* uniformly n = 27 (foreshadowed by Winward and McArthur, 1995); *A. cana* ssp. *cana,* n = 36 (previously mistakenly reported as n = 9 and n = 18); and *A. bigelovii,* n = 36 (one population, other populations are n = 9 and n = 18) (Table 2, Figs. 4–6). The distribution of ploidy levels







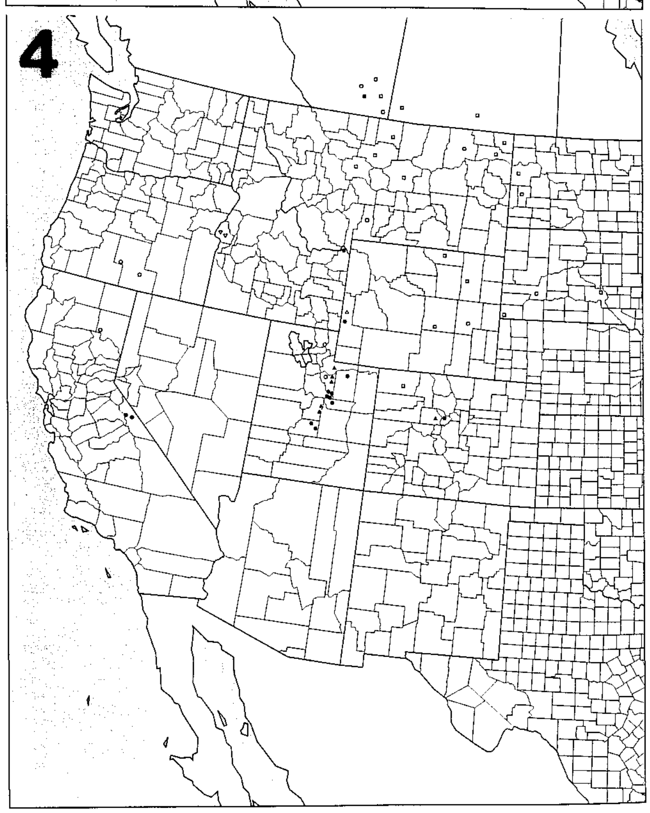


Fig. 1. Distribution of cytotypes of *Artemisia tridentata* ssp. *tridentata* (● = 2*x*, ○ = 4*x*) based on all known chromosome counts (see Table 1 for references).

Fig. 2. Distribution of cytotypes of *Artemisia tridentata* ssp. *vaseyana* (● = 2*x*, ○ = 4*x*) based on all known chromosome counts (see Table 1 for references).

shown in Tables 1 and 2 demonstrates that *Tridentatae* species are mostly 2*x* and 4*x* with 6*x* limited to two species (*A. arbuscula* and *A. rothrockii*) and 8*x* common in only one species (*A. cana*). We recorded the presence of a low frequency of supernumerary or b chromosomes [ten of the 366 populations (2.8%) representing five taxa in Table 2].

General distribution of cytoypes—The geographic distribution of ploidy level or cytotype distribution for each *Tridentatae* species is presented in Figs. 1–6. The distributions of populations of known ploidy levels for the central species of the species complex, *A. tridentata,* are shown in Figs. 1–4 with *A. t* ssp. *tridentata, A. t.* ssp. *vaseyana,* and *A. t.* ssp. *wyomingensis* in Figs. 1, 2, and 3, respectively. All three subspecies are widespread and common. Subspecies *tridentata* and *vaseyana* are both predominantly 2*x* but have substantial numbers of 4*x* populations as well. About three-fourths of ssp. *tridentata* populations are 2*x*; 4*x* populations are scattered throughout the range with notable pockets in north-central Washington extending into south-central British Columbia and in southern California (Fig. 1). Subspecies *vaseyana* populations are 70% 2*x* with the 4*x* populations scattered throughout the distribution range; 4*x* have not been discovered in the Colorado Rockies or in south-central British Columbia (Fig. 2). *Artemisia tridentata* ssp. *wyomingensis* is uniformly 4*x* throughout its extensive range (Fig. 3); earlier counts of 6*x* for two populations have since been shown to be for *A. arbuscula* ssp. *longicaulis* (Winward and McArthur, 1995). The two less common subspecies of *A. tridentata*, ssp. *spiciformis* and *xericensis,* reveal contrasting patterns (Fig. 4). Subspecies *spiciformis* has both 2*x* and 4*x* populations in its high elevation habitats, whereas ssp. *xericensis* is 4*x* in its restricted range in west-central Idaho (Fig. 4). This is the first report for a chromosome number for ssp. *xericensis,* although Winward (1970) speculated that it might be a 2*x* taxon.

The subspecies of *A. cana* like those of *A. tridentata* have contrasting polyploid patterns (Fig. 4). There are two common subspecies of *A. cana*; ssp. *cana* is mostly a Great Plains taxon and ssp. *viscidula* is a high-elevation, mountain taxon. The third subspecies, ssp. *bolanderi* grows in alkaline basins. Subspecies *cana* is 8*x*, a discovery we report for the first time. The solitary 4*x* report by Stahevitch and Wojtas (1988) is suspect since numerous plants in 24 other populations were all 8*x*. Subspecies *viscidula,* on the other hand, includes populations at both the 2*x* and 4*x* levels. The only populations of ssp. *bolanderi* reported is 2*x* (Fig. 4).

The widespread species *A. nova* and *A. arbuscula,* sometimes treated as conspecific (Ward, 1953), include populations at different ploidy levels (Fig. 5). Populations of *A. nova* are about two-thirds 4*x* and one-third 2*x*. Populations of *A. arbuscula* ssp. *arbuscula* are 2*x* and 4*x* in relatively even proportions. Populations of *A. arbuscula* ssp. *longicaulis* are uniformly 6*x* (Fig. 5).

The remaining *Tridentatae* species are less common and more geographically restricted (Fig. 6). Many of these species also include polyploid cytotypes. *Artemisia tripartita, A. rigida,* and *A. longiloba* all have 2*x* and 4*x* populations. *Artemisia bigelovii* has 2*x* and 4*x* populations as well as a single 8*x* population; *A. rothrockii* has 4*x* and 6*x* populations and perhaps one 8*x* population (Clausen, Keck, and Hiesey [1940] recorded a single 8*x* plant but neither Ward [1953] nor McArthur, Pope, and Freeman [1981] confirmed an 8*x* presence). *Artemisia pygmea* populations are 2*x,* although individual plants in one population were 4*x* (McArthur, Pope, and Freeman, 1981). The single report for *A. argillosa* is 4*x.*

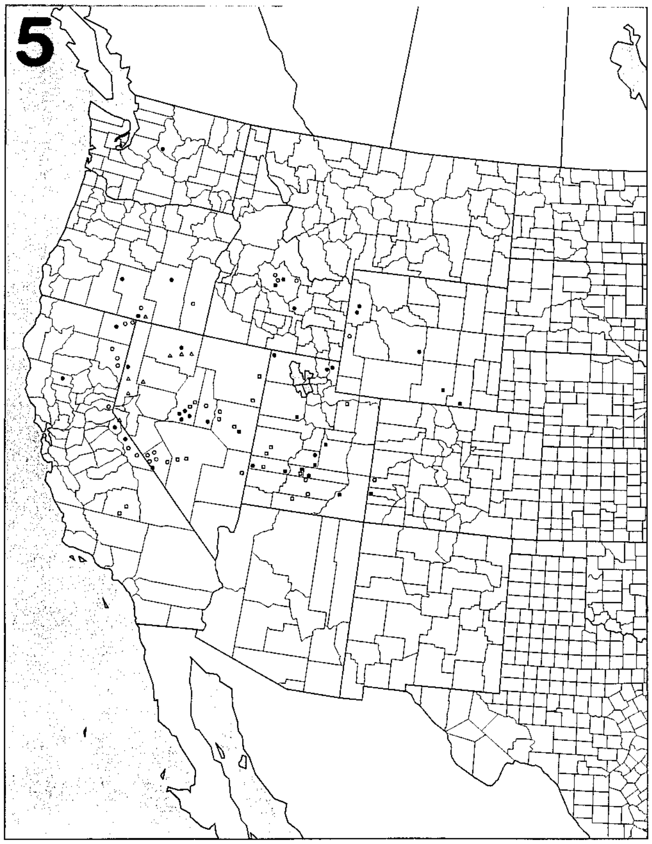
Sympatric or tightly parapatric distribution of cytotypes—Since we usually counted chromosomes from several plants per population (Table 2; $\bar{X}$ = 3.1, range 1–27), we confirmed the earlier account of populations with mixed ploidy levels (McArthur, Pope, and Freeman, 1981). Several populations include both 2*x* and 4*x* plants, i.e., one population of *A. arbuscula* ssp. *arbuscula,* ten populations of *A. tridentata* ssp. *vaseyana,* and a hybrid population of *A. t.* ssp. *tridentata* × *A. t.* ssp. *vaseyana.* One *A. t.* ssp. *vaseyana* population had a 6*x* plant in an otherwise 2*x* population (Table 2). Three of the *A. t.* ssp. *vaseyana* population samples that had 2*x* and 4*x* plants were near Pine Valley Mountain in Washington County, Utah (Fig. 7). In several other locations that taxon has tightly parapatric 2*x* and 4*x* populations, e.g., locations in Washington, Sevier, and Utah counties, Utah (Table 2 and illustrated in Fig. 7).

In many locations taxa at 2*x* and 4*x* are tightly parapatric. This is especially the case with *A. tridentata* ssp. *tridentata* and *wyomingensis.* Locations documented in Table 2 include south of Fredonia, Arizona (ssp. *tridentata* = U-134, ssp *wyomingensis* = U-032), south of Dinosaur, Colorado (M&S 1437, 1438), Baker, Nevada (M&S 1445, 1444), Ely, Nevada (U-120, U-012), Captain Keeney Pass, Oregon (M&S 2318, 2317), Kane Springs, Oregon (M&S 2319, 2320), west of Adrian, Oregon (M&S 2315, 2316), Gordon Creek, Utah (M&S 2180A, 2180B), north of Benton City, Washington (M&S 2336, 2333), north of Medicine Bow, Wyoming (Jones 127, 128) base of North Table Mountain, Wyoming (M&S 1577, 1576), and Patrick Draw, Wyoming (M&S 1571, 1570). The tight parapatric juxtaposition of individual plants at the Dinosaur, Colorado, and North Table Mountain, Wyoming, locations are illustrated in Figs. 8 and 9. The obvious size differences in the taxa (ssp. *tridentata* plants are the large ones) blur somewhat at the ecotone (Figs. 8, 9), but the ecotone is, nevertheless, quite sharp. Height and crown differences at the Dinosaur site are

←

Fig. 3. Distribution of cytologically determined populations of *Artemisia tridentata* ssp. *wyomingensis* (● = 4*x*) based on all known chromosome counts (see Table 1 for references).

Fig. 4. Distribution of cytotypes of *Artemisia cana* (ssp. *viscidula*—● = 2*x*, ○ = 4*x*; ssp. *cana*—■ = 4*x*, □ = 8*x*; and ssp. *bolanderi*—* = 2*x*), *A. tridentata* ssp. *xericensis* (▽ = 4*x*) and *A. t.* ssp. *spiciformis* (▲ = 2*x*, △ = 4*x*) based on all known chromosome counts (see Table 1 for references).



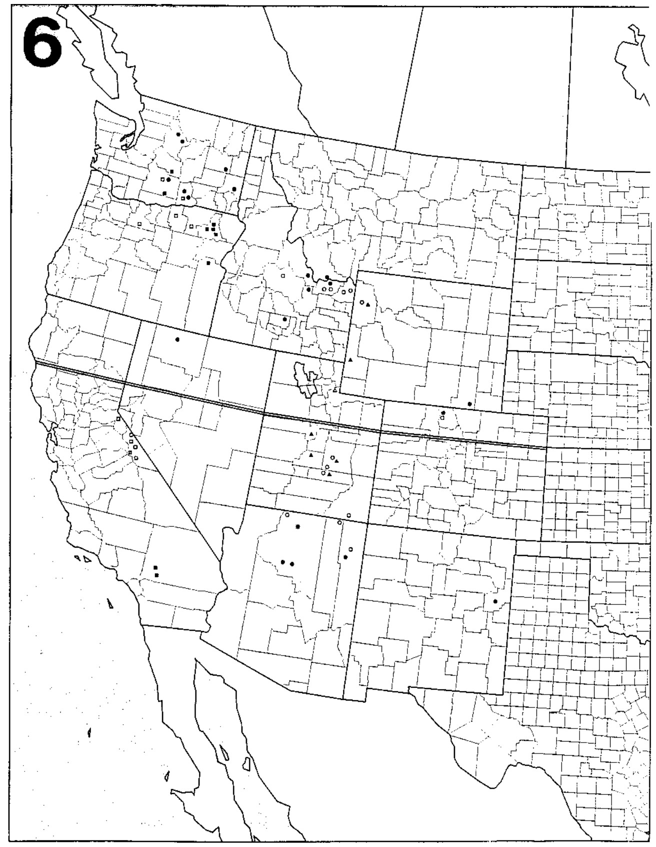


Fig. 5. Distribution of cytotypes of *Artemisia arbuscula* (ssp. *arbuscula*—● = 2*x*, ○ = 4*x*; and ssp. *longicaulis*—△ = 6*x*) and *A. nova* (■ = 2*x*, □ = 4*x*) based on all known chromosome counts (see Table 1 for references).

Fig. 6. Distribution of cytotypes of *Artemisia tripartita* (● = 2*x*, ○ = 4*x*), *A. rigida* (■ = 2*x*, □ = 4*x*), *A. argillosa* (* = 4*x*), and *A. longiloba* (▲ = 2*x*, △ = 4*x*), above the double line; *A. bigelovii* (● = 2*x*, ○ = 4*x*, * = 8*x*), *A. pygmaea* (▲ = 2*x*), and *A. rothrockii* (■ = 4*x*, □ = 6*x*, □ = 8*x*), below the double line. Data are based on all known chromosome counts (see Table 1 for references).

significantly different (height, ssp. *tridentata* = 1.68 ± 0.10 m, ssp. *wyomingensis* = 0.93 ± 0.09 m, $P < 0.001$; crown diameter, ssp. *tridentata* = 1.53 ± 0.15 m, ssp. *wyomingensis* = 0.98 ± 0.09 m, $P < 0.05$, SAS, GLMP). Size differences at North Table Mountain (Fig. 9) are also apparent, but the data were not analyzed because of the small sample size. The Benton City, Washingon, site merits comment. There, mature ssp. *wyomingensis* plants are much larger than ordinary for that taxon, up to 2 m tall but otherwise conform to ssp. *wyomingensis* taxonomic criteria. Mature ssp. *tridentata* plants at that site are very tall, among the tallest, up to 4 m, of the known height range of that taxon (McArthur et al., 1979). Similarly, essentially 2*x* ssp. *vaseyana* and 4*x* ssp. *wyomingensis* interface, e.g., north of Harper, Oregon (M&S 2329A, 2329B), Nash Wash, Utah (M&S 2038, 2036), near Cove Fort, Utah (M&S *s.n.*, August 24, 1984).

At several locations both 2*x* and 4*x* *A. tridentata* ssp. *vaseyana* are in close contact or even intermixed, e.g., Walden, Colorado (M&J U-061), Clover Creek, Oregon (M&S 2328), Martin's Draw, Utah (M&S 1597), Cove Fort, Utah (M&S *s.n.*, August 24, 1984), Salina Canyon, Utah (M&S 2148, 2149, 2150, 2151, 2153), Hobble Creek, Utah, (M&S *s.n.*, October 21, 1987, 1476, 2144, 2363) Pinto Canyon, Utah (M&S 2438, 2439), and Diamond Valley, Utah (M&S 2440) (Table 2). The distribution of individual 2*x* and 4*x* plants from three sites near Pine Valley Mountain, Utah, is presented in Fig. 7. Coumarin concentrations were significantly different ($P < 0.01$) between 2*x* and 4*x* plants of ssp. *vaseyana* in the study as a whole (Table 3). However, in these populations near Pine Valley Mountain, neither height, crown diameter, nor coumarin content could clearly distinguish 2*x* from 4*x* plants. The mean values of plants from the population represented by M&S 2439, which was most numerically balanced for 2*x* and 4*x* individuals (Table 2, Fig. 7), were for height, 2*x* = 0.96 ± 0.11 m and 4*x* = 1.05 ± 0.11 m, for crown diameter, 2*x* = 1.11 ± 0.17 m and 4*x* = 1.26 ± 0.11 m, and for coumarin content, 2*x* = 4.57 ± 0.29 (range = 3–5) and 4*x* = 2.40 ± 0.97 (range 0–4). At the other two sites near Pine Valley Mountain (represented by M&S 2440 and M&S 2438; Table 2, Fig. 7), the values for height, crown diameter, and coumarin levels for the less common ploidy level plants are inconspicuously embedded in the overall population values (data not shown).

Ecotones or taxonomic points of contact—The data presented in Table 2 and Figs. 1–6 demonstrate that *Tridentatae* taxa overlap substantially in general distribution and have numerous points of contact. In this section, we

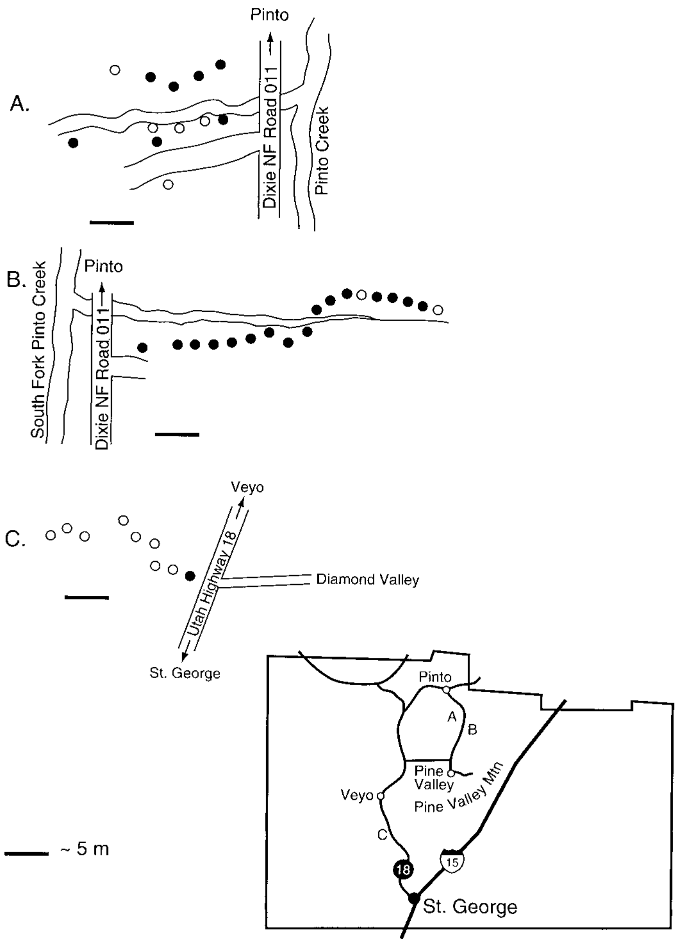


Fig. 7. Mixed ploidy populations of *Artemisia tridentata* ssp. *vaseyana* in the Pine Valley Mountain Area, Washington County, Utah (● = 2*x* plant, ○ = 4*x* plant). Only 2*x* plants are found at Pine Valley, and only 4*x* plants are found at Pinto and at Snow Canyon (south of C).

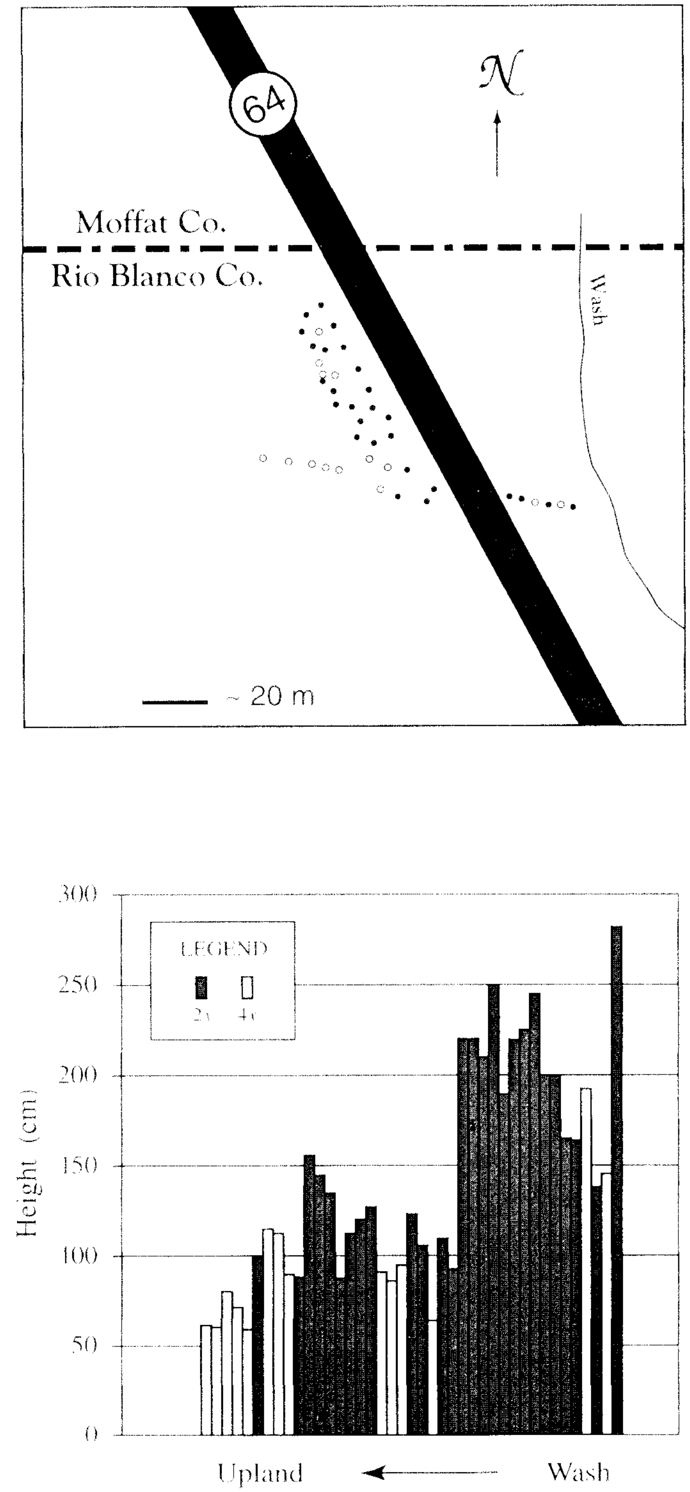


Fig. 8. Distribution and height of *Artemisia tridentata* ssp. *tridentata* (● = 2*x*) and *A. t.* ssp. *wyomingensis* (○ = 4*x*) plants south of Dinosaur, Colorado. Distribution (top). Heights (bottom).

list several recurring patterns aside from the cytotypic or interploidy level data presented in the previous section.

The central species of *Tridentatae*, *A. tridentata*, has numerous inter- and intraspecific contacts, some detailed in the previous section. The three common subspecies, *tridentata*, *vaseyana*, and *wyomingensis*, occasionally tightly co-occur, e.g., Clear Creek Canyon–Cove Fort area, Utah (M&S 1484, 1488, 2085, 2086, 2087, 2088, 2089, *s.n.*, August 24, 1984, August 20, 1992), Martin's Draw, Utah (M&S 1597, 1599, 1603, 1604), and Rio Grande Drainage, Idaho (M&S 2098, 2100, 2102, *s.n.*, July 27, 1992); see also reports from Beetle and Young (1965; Daniel, Wyoming) and Harniss and McDonough (1975; Dubois, Idaho). We did chromosome counts from 69 different plants over a 31 km transect on the Clear Creek and Cove Creek drainages across the Cove Fort Summit of the Pahvant-Tushar Mountain Range axis in south-central Utah (Table 2). On that transect we recorded 12 2*x* ssp. *tridentata*, 22 2*x*, one 4*x*, and one 6*x* ssp. *vaseyana*, and 33 4*x* ssp. *wyomingensis* plants.

In several locations, 2*x* ssp. *tridentata* and ssp. *vaseyana* essentially interface, e.g., Hatch, Utah (U-070, U-031), Salt Creek Canyon, Utah (U-109, M&S 2503, 2504, 2505, 2506, 2507), and north of Kemmerer, Wyoming (M&S 1736, 1737) (Table 2). Several other interfaces from information presented in Table 2, our personal observations, and the literature are: *A. arbuscula* ssp. *arbuscula* and *A. nova* (M&S 2107A, 2107B; Table 2), *A.*

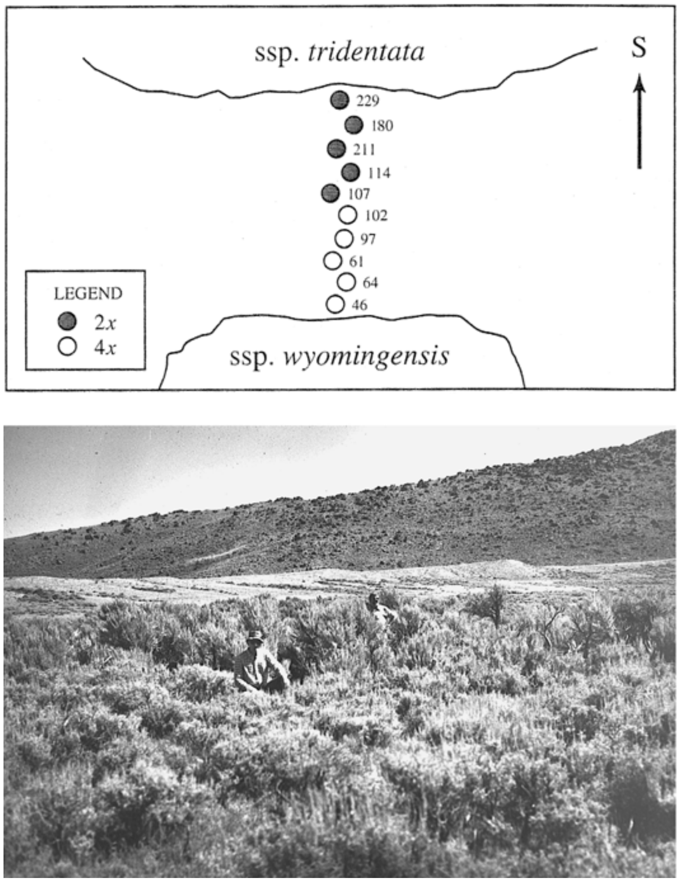


Fig. 9. Distribution, height, and photograph of *Artemisia tridentata* ssp. *tridentata* ($2x$) and *A. t.* ssp. *wyomingensis* ($4x$) at North Table Mountain, Sweetwater County, Wyoming. Transect with heights in centimetres top). Photograph: kneeling and standing gentlemen are both 193 cm tall when standing (bottom).

arbuscula ssp. *arbuscula* and *A. tridentata* ssp. *wyomingensis* (Young *s.n.,* August 24, 1984; Table 2), *A. arbuscula* ssp. *arbuscula* and *A. tridentata* ssp. *vaseyana* (Ward, 1953; McArthur and Sanderson personal observations, head of Logan Canyon, Utah), *A. arbuscula* ssp. *longicaulis* and *A. tridentata* ssp. *wyomingensis* (footnote d, Table 1; Winward and McArthur, 1995), *A. cana* ssp. *cana* and *A. tridentata* ssp. *wyomingensis* (M&S 2113, 2114; 2483, 2484; 2495, 2493), *A. tridentata* ssp. *wyomingensis* and *A. tripartita* ssp. *tripartita* (M&S 2337, 2341, *s.n.,* August 31, 1994, Table 2), *A. tridentata* ssp. *wyomingensis* and *A. nova* (McArthur and Sanderson personal observations, Gabbs, Nevada, Desert Experimental Range, Utah), *A. tridentata* ssp. *vaseyana* and *A. tridentata* ssp. *spiciformis* (several locations in Utah; McArthur and Goodrich, 1986), *A. tridentata* ssp. *vaseyana* and *A. cana* ssp. *viscidula* [Soldier Summit area, Utah (M&S 2132, 2195, 2146), Strawberry Valley, Utah, and other locations; McArthur and Goodrich, 1986; Winkel, 1986].

Coumarin concentrations by ploidy level in A. tridentata—Coumarin concentrations in the three common subspecies of *A. tridentata* reveal some interesting patterns (Table 3). Subspecies *vaseyana* has high concentrations, whereas ssp. *tridentata* and *vaseyana* do not.

TABLE 3. Coumarin concentrations by ploidy levels in the principal *A. tridentata* subspecies.

Taxon	No. of plants	Ploidy level	Coumarin content[a]			
			$\bar{X}$	Range	SE	Signf.[b]
A. t. ssp.	127	$2x$	0.44	0–3	0.05	*
tridentata	8	$4x$	0.88	0–3	0.30	
A. t. ssp.	148	$2x$	4.43	0–5	0.08	**
vaseyana	85	$4x$	2.52	0–5	0.17	
A. t. ssp.						
wyomingensis	110	$4x$	0.36	0–4	0.07	

[a] Determined on a 0–5 scale.
[b] Ploidy levels were compared within subspecies by *t* tests. * $P < 0.05$, ** $P < 0.01$.

Within ssp. *vaseyana* $2x$ plants have significantly higher ($P < 0.01$) coumarin concentrations than $4x$ plants. Conversely, within ssp. *tridentata* $4x$ plants have significantly higher ($P < 0.05$) concentrations than $2x$ plants.

DISCUSSION

Polyploidy—Tridentatae species exhibit abundant polyploidy. All the major species (*A. tridentata, A. cana, A. arbuscula,* and *A. nova*), as well as several less common or more geographically restricted ones (*A. bigelovii, A. longiloba, A. rigida, A. tripartita,* and *A. rothrockii*) include diploid and polyploid populations (Tables 1, 2). Several of the prominent subspecies, e.g., *A. tridentata* ssp. *tridentata, A. t.* ssp. *vaseyana, A. cana* ssp. *viscidula*, and *A. arbuscula* ssp. *arbuscula,* also include polyploid populations, but others do not or have only limited cytotypic differentiation, e.g., *A. tridentata* ssp. *wyomingensis, A. arbuscula* ssp. *longicaulis,* and *A. cana* ssp. *cana.* Other *Artemisia* subgenera also include species with high frequencies of polyploidy (Keck, 1946; Ehrendorfer, 1964; Estes, 1969; Persson, 1974; Stahevitch and Wojtas, 1988). A summary of the literature on intraspecific dicot polyploidy through 1974 (Lewis, 1980a) placed *Artemisia* with 47 cases, second only to *Potentilla* with 60 cases (N = 758 genera). It appears that polyploidy is an important mechanism in the differentiation and adaptation of *Artemisia* species in general and *Tridentatae* species in particular. *Tridentatae* species not only exhibit broad general polyploid patterns (Table 1, Figs. 1–6) but also patterns that are evident at ecotonal interfaces and within populations (Table 2, Figs. 7–9).

The low frequency of supernumerary or b chromosomes present in ten populations (2.8%) of the sampled populations (Table 2) is similar to results reported earlier by Ward (1953) and McArthur, Pope, and Freeman (1981). These results do not appear to be systematically meaningful.

The $2x$–$4x$ population interfaces are quite common. Notable examples are between $2x$ *A. tridentata* ssp. *tridentata* or ssp. *vaseyana* with $4x$ *A. t.* ssp. *wyomingensis.* What might the biological significance of these frequent contacts be? Hagerup (1932) suggested that polyploids were better adapted to extreme ecological environments than were their diploid relatives (= Hagerup's hypothesis). This hypothesis has been supported by several investigators and reviewers working over a broad geographical range (Tischler, 1935; Wulff, 1937; Löve and Löve, 1943; Johnson and Packer, 1965) but disputed by others (Bowden, 1940; Gustafsson, 1948; Stebbins, 1950, 1971; Powell and Sloan, 1975). Stebbins (1950) suggested that increasing polyploid frequencies have resulted from a selective advantage to heterozygous polyploids in unstable environments. Grant (1971) and Lewis (1980b) recognized the validity of Stebbins' suggestion that increased polyploid frequencies do result from unstable environments, but both also acknowledged possible merit in Hagerup's hypothesis. It has been shown that both diploid and polyploid species can have broad ecological adaptation (Stebbins, 1971), of which diploid and octoploid *Fragaria* species are examples (Hancock and Bringhurst, 1978, 1979). In the *Tridentatae* case under consideration, the essential autoploid nature of the group (McArthur, Pope, and Freeman, 1981) is, we believe, consequential. Levin (1983) suggested that ''autopolyploidy alters cytologic, biochemical, genetic, and physiological, and developmental character which (may) provide tolerance beyond limits of diploid progenitors'' and further suggested that metabolism and growth are retarded in polyploid cells, which would lower growth rates and increase drought tolerance. Wentworth and Gornall (1996) with work on *Parnassia* give additional support for wide ecological amplitude of polyploids. *Artemisia tridentata* ssp. *wyomingensis* is smaller and slower growing (McArthur and Welch, 1982; Barker and McKell, 1986; Shumar and Anderson, 1986), grows on drier sites (Winward, 1980; Barker and McKell, 1983; Shumar and Anderson, 1986; Swanson, Simonson, and Buckhouse, 1986) and is subject to greater water stress (Ayre, 1998; Kolb and Sperry, in press) than are ssp. *tridentata* and ssp. *vaseyana.* Another more limited example is on the foothills of Mt. Borah, Idaho, where 2*x* *A. nova* and 4*x* *A. arbuscula* are tightly parapatric. There, *A. nova* is found in the shallow drainages, ~15 cm deep, dissecting the bajadas, which are covered with *A. arbuscula.* This is a fine-scale environmental gradient but as in the case of 4*x* *A. tridentata* ssp. *wyomingensis* interfaces with 2*x* *A. t.* ssp. *tridentata* and *vaseyana* the 4*x* plants are in the drier habitat. Stutz (1989) suggested that woody polyploids might have reduced stature because of the slowed tempo of cell divisions with consequential additional cellulose deposition in meristematic cells—cells of polyploids in comparison to those of diploids tend to have slower mitotic cycles (Stebbins, 1950, 1971; Grant, 1971). Li, Berlyn, and Ashton (1996) ascribe the drought tolerance of polyploid *Betula* to physiological and morphological adaptations. The subgenus *Seriphidium* species, *Artemisia santonicum,* includes fast-growing diploids and slower growing polyploids (Persson, 1974). Several shrubby genera in addition to *Artemisia* display the syndrome of smaller, drought-tolerant polyploids in comparison to diploids. These include *Atriplex, Chrysothamnus,* and *Larrea* (Yang, 1970; Stutz, Melby, and Livingston, 1975; Sanderson, McArthur, and Stutz, 1989). The condition of smaller polyploids is a reversal of the gigas growth habit of polyploid herbaceous plants (Smith, 1946; Lewis, 1980b). We believe the reversal of the traditional gigas syndrome of large, robust polyploids in herbaceous lineages to large robust diploids and smaller polyploids in some shrubby lineages is a consequence of slower woody plant cellular growth. Two exceptions to the gigas diploid shrub syndrome are instructive. Both *Grayia brandegei* and *Gutierrezia sarothrae* are suffrutescent shrubs with larger polyploids than diploids, thus conforming to the traditional herbaceous gigas syndrome (Solbrig, 1977; Stutz and Sanderson, 1983; Stutz et al., 1987).

Mixoploidy in the form of some plants at higher ploidy levels, usually 4*x,* in otherwise diploid populations but occasionally minority 2*x* plants in predominant 4*x* populations, is quite common in *Tridentatae* populations (McArthur, Pope, and Freeman, 1981; Table 2). We suspect there is a relatively high frequency of unreduced gametes formed, thus producing the higher euploid plants (few odd-ploid, 3*x,* 5*x,* etc. plants have been discovered, but see McArthur, Pope, and Freeman, 1981). Unreduced gametes are the most common mechanism for the production of polyploidy either by direct fusion or self-fertilized progeny of tetraploid chimeras in floral structures (Lewis, 1980b). Unreduced gametes have been shown to be relatively common in the polyploid Anthemideae genus *Achillea,* an *Artemisia* relative (Tyrl, 1975; Vetter et al., 1996). Additional support for the in situ de novo production of 4*x* plants in 2*x* populations is found in the sympatric distributions of plants of these cytotypes in populations of *Artemisia tridentata* ssp. *vaseyana* (Fig. 7). The recent origin of these plants is supported by randomly amplified polymorphic DNA analysis (RAPD). In the same general area shown in Fig. 7, McArthur et al. (1998b) demonstrated that 2*x* and 4*x* plants had the same RAPD profile in addition to being indistinguishable morphologically and chemically (coumarin compound content). The close indistinguishable relationship of the sympatric 2*x* and 4*x* ssp. *vaseyana* plants in the Pine Valley Mountain area (Fig. 7) by RAPD analysis together with overall close relationships of ssp. *vaseyana* from all locations and indeed of all *A. tridentata* and of subgenus *Tridentatae* in hierarchical order support the autopolyploid nature of the *Tridentatae* (McArthur et al., 1998b,c). Previous work in our laboratory supported the autopolyploid nature of *Tridentatae* based on similarity of 2*x* karyotypes and the 4*x* karyotypes being approximate doubles of the 2*x* ones, a high frequency of multivalents in pollen mother cells of polyploids, and mixed ploidy populations (McArthur, Pope, and Freeman, 1981).

Tridentatae evolution—The differentiation of *Tridentatae* taxa by polyploidy and hybridization has apparently led to a widely successful plant group consisting of a large species complex. Polyploidization has apparently provided new genetically isolated material for selective forces to mold. Hybridization is widespread in the *Tridentatae* (Hall and Clements, 1923; Ward, 1953; Beetle, 1960; McArthur, Welch, and Sanderson, 1988; Weber et al., 1994). Several extant taxa are thought to be the products of hybridization events, some also involving polyploidization as well (Ward, 1953; Beetle and Young, 1965; McArthur and Goodrich, 1986; Winward and McArthur, 1995). Kornkven (1997) and Kornkven, Watson, and Estes (1998) suggest that the non-*Tridentatae* species *A. filifolia* (subgenus *Dracunculus*) may have a reticulate relationship with the *Tridentatae.* They suggest that the *Tridentatae* chloroplast genome has been captured by *A. filifolia.* McArthur and Pope (1979) reported that the karyotype of *A. filifolia* is similar to the *Tridentatae* karyotype, more similar, in fact, than it is to *A. spinescens*, a member of subgenus *Dracunculus* as is *A. filifolia.* Torrance and Steelink (1974) reported that the sesquiterpene lactone colartin common in several *Tridentatae* species is present in *A. filifolia.* Perhaps the relationship of *A. filifolia* is closer to the *Tridentatae* than has been previously assumed.

In a series of studies on hybrid zones (Harrison, 1993; Arnold et al., 1999), McArthur, Freeman, Graham, and colleagues have shown that the *A. tridentata* ssp. *tridentata*—*A. t.* ssp. *vaseyana* hybrid zone is stable and contains a reservoir of fit hybrid plants (Freeman et al., 1991, 1995, 1999; Graham, Freeman, and McArthur, 1995; Messina, Richards, and McArthur, 1996; Wang et al., 1997, 1998, 1999; McArthur et al., 1998a; McArthur and Sanderson, 1999). Such *Tridentatae* hybrid zones could have been the source for differentation of new genetic combinations that were able to exploit new habitats available as climates changed in the Pliocene and Pleistocene when the *Tridentatae* apparently differentiated and became important landscape dominants (McArthur and Plummer, 1978; McArthur et al., 1981; Thompson, 1991). Couple the successful and stable *Tridentatae* hybrid zone formation with the group's inherent propensity for polyploidization and, we believe, a formula for success has been achieved: the landscape dominant subgenus *Tridentatae.*

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