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American Journal of Botany, Volume 76, Issue 5 (May, 1989), 679-691.

Stable URL:
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Amer. J. Bot. 76(5): 679–691. 1989.

PATTERNS OF ISOZYME VARIATION IN WESTERN NORTH AMERICAN ANTENNARIA (ASTERACEAE: INULEAE) II. DIPLOID AND POLYPLOID SPECIES OF SECTION ALPINAE[1]

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ABSTRACT

Antennaria is a genus of dioecious, perennial, herbaceous Composites that are especially diverse in the cordillera of western North America. Section *Alpinae* consists of about nine taxa, among them *A. aromatica, A. densifolia, A. media, A. pulchella,* and *A. umbrinella.* Although diploids are morphologically distinct, the polyploid derivatives of the diploids obscure the morphological distinctness of the groups. A survey of 19 putative isozyme loci indicates that the diploids have diverged only moderately from one another with respect to biochemical genetics ($I = 0.838$ to 0.961). Additionally, only moderate amounts of genetic diversity were detected. Isozyme data are supportive of a hypothesis of a rapid mode of speciation in *Antennaria,* where morphological differentiation has been accompanied by small amounts of allozyme divergence. Polyploids have significantly higher amounts of heterozygosity than diploids and tetrasomic inheritance is inferred. Evidence from morphology and biochemical genetics suggests that the polyploids represent a continuum between interracial autopolyploids and segmental allopolyploids. In light of the relatively low degree of genetic and morphological divergence among many *Antennaria* species, taxonomic conservatism is advocated.

ANTENNARIA Gaertner section *Alpinae* comprises a group of several sexually reproducing diploid-polyploid species as well as a large polyploid agamic complex. Several of the sexually reproducing species, namely *A. aromatica* Evert, *A. densifolia* A. E. Porsild, *A. media* Greene, *A. pulchella* Greene, and *A. umbrinella* Rydb., are related to polyploids in the *A. alpina* (L.) Gaertn. and *A. rosea* Greene agamic complexes (Bayer, 1987a). The taxonomy of this group of species has been in dispute because of morphological intergradation among several of the species.

Antennaria aromatica is a recently described species (Evert, 1984) from western Montana, areas of Wyoming adjacent to Yellowstone National Park, and portions of Alberta and British Columbia immediately adjacent to Montana (Fig. 2). It is most prevalent in the front ranges of the Rocky Mountains, where it occurs primarily on limestone talus from treeline to alpine tundra, is known from only about 30 sites, and includes diploid and tetraploid races. *Antennaria umbrinella* is a species of wide distribution, commonly found in the front ranges of the Rocky Mountains from Colorado to Alberta, decreasing in frequency in the western portions of its range into British Columbia, Washington, and Oregon (Fig. 1; Bayer and Stebbins, 1987). Typically a plant of lower elevations, occurring in Ponderosa woodlands and sagebrush steppe, *A. umbrinella* occasionally grows nearly to timberline. It is taxonomically problematic because in some areas it intergrades morphologically into *A. media* sensu lato (Bayer, 1987b). *Antennaria umbrinella* has both diploid and tetraploid cytotypes (Bayer and Stebbins, 1987). *Antennaria pulchella* and *A. media* sensu stricto are the diploid and polyploid cytotypes respectively of *A. media* sensu lato (Bayer, 1987b). *Antennaria pulchella* is morphologically distinct from *A. media* sensu stricto and therefore probably should be recognized at the rank of species (Bayer, unpublished data). Additionally, *A. pulchella* is restricted to the alpine of the Sierra Nevada Mountains, while *A. media* is a widely distributed alpine species from New Mexico and Arizona north to Yukon and Alaska (Fig. 2; Bayer and Stebbins, 1987). *Antennaria densifolia* is an obscure species which occurs principally on the unglaciated eastern slopes of the Mackenzie

[1] Received for publication 19 May 1988; revision accepted 7 November 1988.

This research was funded by grants from the Natural Sciences and Engineering Research Council of Canada (NSERC grant #s A2924 and A3797) and by a University of Alberta Central Research Fund Grant (NSERC). Thanks go to Rob DeLuca, Mark Joncas, Klaus Lackschewitz, Dan Lebedyk, Ledyard Stebbins, and Krystyna Urbanska for accompanying me in the field on several occasions. Rob DeLuca, Mark Joncas, and Dan Lebedyk are acknowledged for their assistance in the lab. I express gratitude to Keith Denford and Doug Soltis for their careful reviews of this paper.

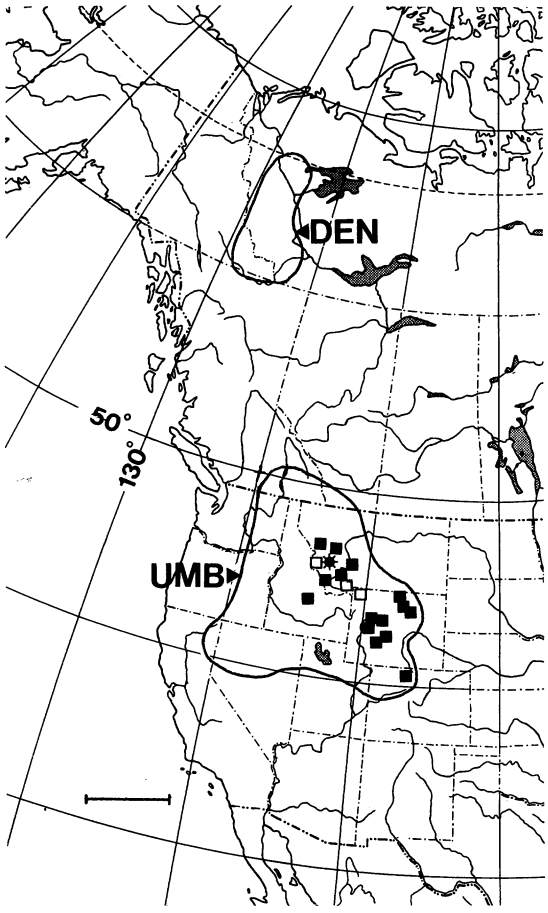

Fig. 1. Ranges of *Antennaria umbrinella* and *A. densifolia* and positions of 19 populations of the two species in relation to their ranges. The margins of the known ranges of the two taxa are labeled with the first three letters of their specific epithets. One diploid population of *A. densifolia* occurs within the range of *A. umbrinella* and is disjunct from the primary range of the species in subarctic Canada. Individual populations are labeled as follows: (✱) *A. densifolia,* (□) *A. umbrinella* (diploids), and (■) *A. umbrinella* (tetraploids). Bar equals 500 km.

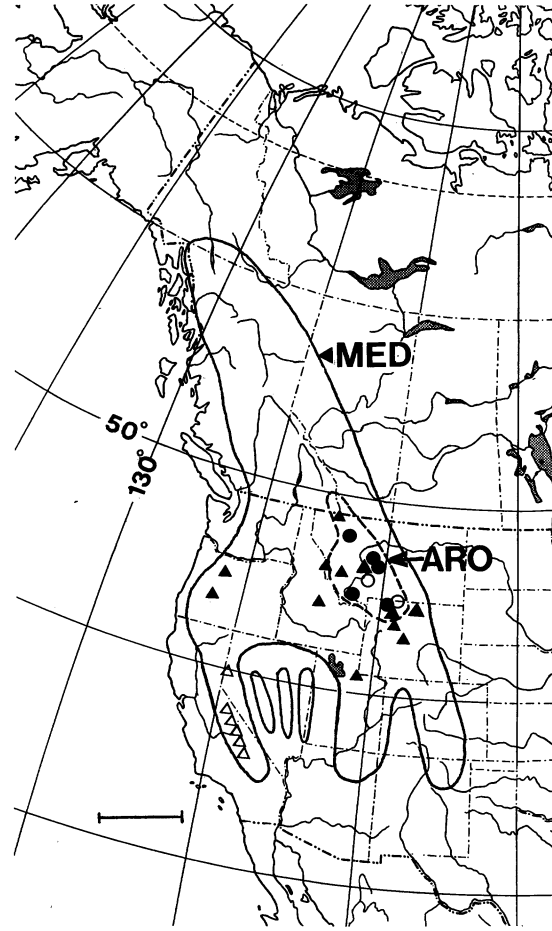

Fig. 2. Ranges of *Antennaria aromatica* and *A. media* sensu lato and positions of 25 populations of the two species in relation to the ranges. The margins of the known ranges of the two taxa are labeled with the first three letters of their specific epithets. Individual populations are labeled as follows: (○) *A. aromatica* (diploids), (●) *A. aromatica* (tetraploids), (△) *A. media* (= *A. pulchella*) (diploids), and (▲) *A. media* sensu stricto (tetraploids). Bar equals 500 km.

Mountains of the Northwest Territories and Yukon Territory (Porsild, 1945; Rutter, 1984). Its chromosome number is unknown, but measurements of pollen grains and guard cells suggest it to be diploid (Bayer, unpublished data). Recently, plants were found in a remote area of Granite Co., Montana, that are very similar to specimens of *A. densifolia* from subarctic Canada, except that the Montana plants are somewhat shorter in height. This population is disjunct from the Canadian populations by about 2,000 km (Fig. 1). Plants from this population are diploid ($2n = 28$; Bayer, unpublished data). Descriptions of the habitat of the populations in the Northwest Territories (Porsild, 1945), dry limestone talus in the alpine zone, match those of the Montana site.

All of the taxa discussed above are sexually reproducing, having roughly equal frequencies of staminate and pistillate clones in their populations, except for several asexual (gametophytic apomixis) populations of *A. media* sensu stricto and one of *A. aromatica* (Appendix). The degree of morphological divergence having been already assessed, the primary purpose of this investigation was to ascertain the degree of genetic divergence among the species and compare it with the degree of morphological divergence among them. Additionally, information about the origin of the polyploids, as

well as differences in the genetic structure of populations of diploids and polyploids was sought. Some meaningful questions that will be addressed are: How does the degree of allozyme divergence compare with the morphological divergence among species? To what degree have the diploids diverged genetically from each other? What evidence exists for an autopolyploid versus an allopolyploid origin for the polyploids? How does the level of genetic variation in the polyploids compare with that of the diploids? Are the levels of heterozygosity in the polyploids significantly different from those of the diploids?

MATERIALS AND METHODS—Plants were studied from 44 populations of *A. aromatica* (seven populations; two diploid and five tetraploid; total of 138 individuals), *A. densifolia* (one diploid population; total of 28 individuals), *A. media* sensu lato (18 populations; six diploid and 12 tetraploid; total of 300 individuals), and *A. umbrinella* (18 populations; three diploid and 15 tetraploid; total of 315 individuals). An attempt was made to choose populations from over the entire range of each species. Diploid populations of *A. aromatica, A. media,* and *A. umbrinella* are much less frequent than polyploid populations and therefore more difficult to locate for study. Generally, portions of plants in the field were removed and transplanted to cultivation because seeds are only available for a limited time before they disperse. When ripe seeds were available, they were gathered from 30+ clones and handled as a bulk collection. In either situation, seedlings, or ramets, collected from the field were cultivated in the University of Alberta Phytotron until they were ready for analysis.

Methodologies are almost identical to those used in previous studies of *Antennaria* (Bayer and Crawford, 1986; Bayer, 1988). Actively growing leaves or flower heads were used for electrophoresis. Plant materials were ground in ice-cold tris-HCl extracting buffer: 0.1 M trics-HCl, pH 7.5, 4.0 mM 2-mercaptoethanol, 1.0 mM EDTA (disodium salt), 10.0 mM KCl, and 10.0 mM $MgCl_2$ (Gottlieb, 1981b). About 20 mg of polyvinyl-polypyrrolidone (Sigma P6755) was added to each sample at the time of grinding, to improve resolution of the enzymes. Filter paper wicks were saturated with supernatant before being loaded into 12.5% starch gels. Two buffer systems were used: 1) general protein (GP), glutamate dehydrogenase (GDH), leucine aminopeptidase (LAP), phosphoglucoisomerase (PGI), superoxide dismutase (SOD), and triosephosphate isomerase (TPI) were resolved on a system composed of a gel buffer consisting of 1 part 0.038 M lithium hydroxide·H_2O-0.188 M boric acid (pH 8.2), and 9 parts 0.05 M tris-0.007 M citric acid (pH 8.4), with the electrode buffer containing only the lithium borate component, and 2) acid phosphatase (ACP), malate dehydrogenase ((NAD) MDH), phosphoglucomutase (PGM), and shikimic acid dehydrogenase (SKDH) were assayed on a system consisting of a gel buffer of 0.016 M L-histidine (free base) and 0.002 M citric acid·H_2O (pH 6.5), and an electrode buffer of 0.065 M L-histidine (free base)-0.007 M citric acid·H_2O (pH 6.5) (Cardy, Stuber, and Goodman, 1981). Procedures used for the visualization of all enzymes followed Soltis et al. (1983), except for general protein (GP) in which the gel was stained with a solution containing 5 parts methanol, 5 parts water, 1 part acetic acid, and 100 mg/100 ml Brilliant Blue G stain. After incubation from 30 min at 37.0 C, the gel was destained with a solution of the same composition excluding the stain component. Although it would have been useful to survey additional enzyme systems, either low enzyme activity, uninterpretable enzyme patterns, or unsatisfactory resolution precluded their use in this study.

Pollen leachates and chloroplast extracts, useful in determining the subcellular location of isozymes, were prepared according to protocols of Gastony and Darrow (1983), and Weeden and Gottlieb (1980a, b). These extracts were assayed for PGI, PGM, and TPI on a continuous cellulose acetate gel system using a 0.024 M tris-0.19 M glycine, pH 8.4 buffer system (Bayer, LaDuke, and Crawford, 1987; Bayer, 1988). Electrophoresis was carried out at 200 v (constant) for 25 min at 4.0 C and stain assays utilizing agarose overlays followed Soltis et al. (1983), but using half quantities of all ingredients.

The locus specifying the most anodal isozyme was designated as 1, the next 2, and so on (locus designations are the same as those given in Bayer and Crawford, 1986). In a similar manner, the most anodal allozyme at a given gene was labeled A, etc.

Genetic variation, such as number of alleles per locus (A) (including monomorphic loci), proportion of loci polymorphic (P), observed and expected average heterozygosities (H_{obs} and H_{exp} respectively) were evaluated. The observed and expected average heterozygosities were compared using χ^2 tests to determine if the natural populations deviated from Hardy-Weinberg equilibruim expectations. T tests (Dixon, 1981) were used to compare mean values of several genetic statistics.

Gene diversity statistics, and standard ge-

TABLE 1. *Genetic variation in 44 populations of* Antennaria *section* Alpinae. *Included are: mean number of alleles per locus (A); proportion of polymorphic loci, where the frequency of the most common allele is less than 0.99 (P); observed average heterozygosity ($H_{(obs)}$); and expected average heterozygosity ($H_{(exp)}$). Population designations are given in the Appendix. Values of $H_{(obs)}$ and $H_{(exp)}$ are not significantly different at the 5% level*

Population designations	A	P	$H_{(obs)}$	$H_{(exp)}$
A. aromatica (diploid)				
A1	1.25 ± 0.578	0.13	0.053	0.063
A2	1.20 ± 0.414	0.20	0.135	0.088
averages	1.23 ± 0.035	0.16	0.094	0.075
(±SD)		(±0.05)	(±0.058)	(±0.018)
A. aromatica (polyploids)				
A3	1.40 ± 0.632	0.33	0.163	—
A4	1.40 ± 0.737	0.29	0.146	—
A5	1.13 ± 0.352	0.13	0.129	—
A6	1.69 ± 1.138	0.29	0.145	—
A7	1.25 ± 0.447	0.27	0.145	—
averages	1.37 ± 0.209	0.26	0.146	—
(±SD)		(±0.08)	(±0.012)	
A. densifolia (diploid)				
D1	1.13 ± 0.516	0.07	0.016	0.021
A. media (diploids)				
M1	1.33 ± 0.724	0.20	0.043	0.049
M2	1.33 ± 0.617	0.27	0.085	0.064
M3	1.25 ± 0.577	0.19	0.079	0.068
M4	1.25 ± 0.577	0.18	0.052	0.049
M5	1.50 ± 0.730	0.29	0.099	0.089
M6	1.13 ± 0.342	0.13	0.036	0.028
averages	1.30 ± 0.123	0.21	0.066	0.058
(±SD)		(±0.062)	(±0.025)	(±0.021)
A. media (polyploids)				
M7	1.31 ± 0.479	0.31	0.092	—
M8	1.23 ± 0.439	0.23	0.231	—
M9	1.13 ± 0.342	0.13	0.124	—
M10	1.23 ± 0.439	0.23	0.231	—
M11	1.17 ± 0.578	0.09	0.083	—
M12	1.25 ± 0.447	0.25	0.250	—
M13	1.31 ± 0.704	0.19	0.119	—
M14	1.31 ± 1.014	0.13	0.023	—
M15	1.00 ± 0.000	0.00	0.000	—
M16	1.38 ± 0.650	0.31	0.212	—
M17	1.31 ± 0.704	0.20	0.063	—
M18	1.27 ± 0.594	0.20	0.097	—
averages	1.24 ± 0.102	0.19	0.127	—
(±SD)		(±0.091)	(±0.085)	
A. umbrinella (diploids)				
U1	1.46 ± 0.776	0.31	0.065	0.084
U2	1.40 ± 0.910	0.20	0.080	0.096
U3	1.38 ± 0.650	0.31	0.138	0.108
averages	1.41 ± 0.416	0.27	0.094	0.096
(±SD)		(±0.062)	(±0.039)	(±0.012)
A. umbrinella (polyploids)				
U4	1.50 ± 0.759	0.36	0.170	—
U5	1.50 ± 1.019	0.21	0.162	—
U6	1.08 ± 0.289	0.08	0.028	—
U7	1.56 ± 0.964	0.31	0.104	—
U8	1.64 ± 1.008	0.36	0.215	—
U9	1.57 ± 1.089	0.29	0.119	—
U10	1.53 ± 0.915	0.33	0.073	—
U11	1.62 ± 0.870	0.39	0.101	—
U12	1.57 ± 1.016	0.29	0.124	—
U13	1.58 ± 1.083	0.27	0.115	—
U14	1.27 ± 0.594	0.20	0.153	—

TABLE 1. *Continued*

Population designations	A	*P*	$H_{(obs)}$	$H_{(exp)}$
U15	1.53 ± 0.915	0.27	0.156	—
U16	1.43 ± 0.814	0.25	0.112	—
U17	1.64 ± 1.008	0.36	0.175	—
U18	1.46 ± 0.776	0.31	0.250	—
averages	1.49 ± 0.149	0.29	0.137	—
(±SD)		(±0.078)	(±0.055)	
Grand averages				
All diploids	1.30 ± 0.120	0.21	0.073	0.067
(±SD)		(±0.076)	(±0.037)	(±0.027)
All polyploids	1.38 ± 0.183	0.25	0.135	—
(±SD)		(±0.092)	(±0.063)	
Both	1.36 ± 0.171	0.23	0.118	—
(±SD)		(±0.089)	(±0.632)	

netic distances and identities were calculated following the methods of Nei (1972, 1973). Nei's statistics were calculated by the GENESTAT program (Whitkus, 1985). The SAHN subroutine of the NTSYS-pc (Rohlf, 1987) program was used to produce phenograms, based on *D* values, by the unweighted pair-group method (UPGMA; Sneath and Sokal, 1973).

Reproductive mode, i.e., whether the population is sexually reproducing or asexual, was inferred by gender ratio determinations in the field. Sexual populations have gender ratios of 1 staminate : 1 pistillate, while asexual ones, reproducing by gametophytic apomixis, consist entirely of pistillate plants (Bayer and Stebbins, 1983). Chromosome numbers were obtained from the populations using methods outlined previously (Bayer, 1984; Bayer and Stebbins, 1987).

RESULTS—The 44 populations used in this study are presented (Appendix) along with locality data (including elevation, latitude, and longitude of the site), chromosome numbers of individuals, collectors and collection numbers, and reproductive mode. The ranges of each of the species are presented in Fig. 1 and 2 along with the location of each of the 44 sites with respect to the ranges.

The 10 enzyme systems that were assayed in this study are believed to be coded by 19 loci. The interpretation of the genetic basis of the enzyme phenotypes has been inferred based on segregation patterns observed at putative loci in plants from natural populations. ACP-1-(A to C), GDH-1-(A and B), GP-1-(A), LAP-1-(A to F), LAP-2-(A to E), MDH-1-(A), MDH-2-(A), MDH-3-(A), MDH-4-(A), PGI-1-(A), PGI-2-(A), PGI-3-(B to E), PGM-1-(A and B), SKDH-1-(A to C), SOD-1-(A), SOD-2-(A), TPI-1-(A and B), TPI-2-(A), and TPI-3-(A to F) are the 19 isozymes (and their allozymes) that were detected. Several unresolved isozymes of ACP were detected on many gels. The complex phenotypes seen at PGM-2 are possibly the result of a locus duplication and make determination of the genotypes impossible at present. The number of isozymes found for each enzyme system, as well as the subcellular localization of several isozymes and the apparent gene duplication for the chloroplast forms of enzyme in PGI and TPI in *Antennaria,* is discussed in Bayer (1988).

Several loci exhibited polymorphism in some or all of the taxa, but others, including *Gp-1* (GP activity consisted of a single monomorphic band in all taxa investigated and is interpreted as a single monomorphic locus), *Mdh-1, Mdh-2, Mdh-3, Mdh-4, Pgi-1, Pgi-2, Sod-1, Sod-2,* and *Tpi-2* were monomorphic in all 44 populations. The table of allelic frequencies is too large to be presented here, but the author will supply it upon request.

Various genetic statistics have been used to assess the degree of genetic variation in *Antennaria* with the intention of comparing genetic variation in *Antennaria* to that in other plant groups. The mean number of alleles per locus (*A*) ranges from 1.00 (locus monomorphic) to 1.69 with a mean for all populations of 1.36. The diploid populations of all species have a mean *A* of 1.30, whereas the polyploid populations have a mean *A* of 1.38 (Table 1). Values for *P* range from 0.00 (all loci monomorphic) to 0.39 (Table 1). The average value of *P* for all populations is 0.23, for all diploid populations 0.21, and for pooled polyploids 0.25. Ranges in H_{obs} are from 0.00 to 0.25 with an average for all populations of 0.118 (Table

TABLE 2. *Nei's genetic diversity statistics for individual taxa and section* Alpinae *(i.e., all taxa). Presented are gene diversities for individual polymorphic loci and pooled loci. Only taxa displaying polymorphism at a given locus are represented; monomorphic loci have gene diversity statistics values of 0.000.* H_T = *total gene diversity within a taxon,* H_S = *gene diversity within populations of a taxon,* D_{ST} = *gene diversity between populations within a taxon,* G_{ST} = *coefficient of gene differentiation*

Loci	Taxa	H_T	H_S	D_{ST}	G_{ST}
Acp-1	*A. aromatica* (4*x*)	0.251	0.183	0.068	0.269
	A. media (2*x*)	0.112	0.111	0.001	0.016
	A. media (4*x*)	0.221	0.096	0.125	0.564
	A. umbrinella (2*x*)	0.220	0.220	0.000	0.000
	A. umbrinella (4*x*)	0.142	0.123	0.019	0.044
	All taxa	0.286	0.213	0.073	0.257
Lap-1	*A. aromatica* (2*x*)	0.542	0.542	0.000	0.000
	A. aromatica (4*x*)	0.407	0.290	0.117	0.287
	A. media (2*x*)	0.487	0.050	0.437	0.897
	A. media (4*x*)	0.607	0.276	0.331	0.545
	A. umbrinella (2*x*)	0.766	0.592	0.174	0.227
	A. umbrinella (4*x*)	0.615	0.429	0.186	0.302
	All taxa	0.658	0.332	0.327	0.496
Lap-2	*A. densifolia* (2*x*)	0.420	0.420	0.000	0.000
	A. media (2*x*)	0.343	0.287	0.056	0.165
	A. umbrinella (4*x*)	0.660	0.666	0.000	0.000
	All taxa	0.246	0.186	0.059	0.242
Pgi-3	*A. aromatica* (2*x*)	0.498	0.236	0.262	0.526
	A. aromatica (4*x*)	0.500	0.430	0.070	0.141
	A. media (2*x*)	0.196	0.185	0.011	0.059
	A. media (4*x*)	0.209	0.209	0.000	0.000
	A. umbrinella (2*x*)	0.112	0.103	0.009	0.078
	A. umbrinella (4*x*)	0.288	0.255	0.033	0.115
	All taxa	0.298	0.255	0.043	0.144
Skdh-1	*A. aromatica* (4*x*)	0.084	0.082	0.002	0.020
	A. media (2*x*)	0.130	0.118	0.012	0.089
	A. media (4*x*)	0.014	0.014	0.000	0.000
	A. umbrinella (2*x*)	0.480	0.408	0.072	0.151
	A. umbrinella (4*x*)	0.440	0.409	0.031	0.071
	All taxa	0.244	0.179	0.045	0.200
Tpi-1	*A. media* (4*x*)	0.481	0.022	0.459	0.955
Tpi-3	*A. aromatica* (2*x*)	0.381	0.348	0.033	0.088
	A. aromatica (4*x*)	0.364	0.329	0.035	0.096
	A. media (2*x*)	0.391	0.350	0.041	0.104
	A. media (4*x*)	0.527	0.434	0.093	0.177
	A. umbrinella (2*x*)	0.203	0.145	0.058	0.287
	A. umbrinella (4*x*)	0.244	0.190	0.054	0.221
	All taxa	0.407	0.296	0.111	0.274
All loci	*A. aromatica* (2*x*)	0.075	0.060	0.016	0.032
	A. aromatica (4*x*)	0.085	0.069	0.016	0.043
	A. densifolia (2*x*)	0.022	0.022	0.000	0.000
	A. media (2*x*)	0.087	0.058	0.029	0.070
	A. media (4*x*)	0.108	0.056	0.052	0.118
	A. umbrinella (2*x*)	0.093	0.077	0.016	0.039
	A. umbrinella (4*x*)	0.142	0.123	0.019	0.044
	All diploids	0.134	0.067	0.067	0.137
	All polyploids	0.125	0.081	0.044	0.118
	All taxa	0.136	0.078	0.058	0.134

1). Average H_{obs} for all diploid populations is 0.073, whereas H_{obs} has an average value of 0.135 for all polyploid populations. Expected values of average heterozygosity (H_{exp}) were calculated only for the diploid populations, because polyploid populations, many of which are asexual, violate assumptions of the Hardy-Weinberg law (Hartl, 1980). The Hardy-Weinberg model assumes that the plants are diploid and that reproduction is sexual. The observed

TABLE 3. *Intraspecific mean genetic distances and mean genetic identities for 3 species of* Antennaria *and pooled groups of diploids and polyploids. Each species is composed of both diploid and polyploid cytotypes*

Taxa	Mean identity (range)	Mean distance (range)
A. aromatica (2*x*)	0.963 (0.963–0.963)	0.037 (0.037–0.037)
A. aromatica (4*x*)	0.977 (0.954–0.996)	0.023 (0.004–0.047)
A. media (2*x*)	0.957 (0.919–0.996)	0.045 (0.004–0.084)
A. media (4*x*)	0.906 (0.837–0.989)	0.100 (0.011–0.177)
A. umbrinella (2*x*)	0.956 (0.947–0.973)	0.045 (0.027–0.054)
A. umbrinella (4*x*)	0.973 (0.894–0.996)	0.028 (0.004–0.112)
All diploids	0.898 (0.805–0.996)	0.109 (0.004–0.217)
All polyploids	0.927 (0.764–0.996)	0.077 (0.004–0.269)

heterozygosities (H_{obs}; Table 1) for the diploid populations were not significantly different from Hardy-Weinberg expectations (H_{exp}; Table 1).

Gene diversity statistics (Nei, 1973) for individual and pooled taxa are presented in Table 2. The statistics are related by the following sets of equations: total gene diversity (H_T) = gene diversity within populations (H_S) + gene diversity between populations (D_{ST}). The coefficient of gene diversity, $G_{ST} = D_{ST}/H_T$. The five highest values for H_T for all populations occur at *Lap-1, Tpi-1, Tpi-3, Pgi-3,* and *Acp-1* (from the highest to the lowest) (Table 2). Highest values for H_T with respect to all loci are found in tetraploid populations of *A. umbrinella,* whereas the lowest total diversity occurs in the population of diploid *A. densifolia* (Table 2). The lowest value of H_T for tetraploid populations (*A. aromatica*) is nearly as high as the highest value for diploid populations (*A. umbrinella*) (Table 2). Additionally, all diploid populations together have an H_T value of 0.134, whereas all polyploids have a value of 0.125 (Table 2).

Nei's measures of intraspecific mean genetic distance (*D*) and identity (*I*) (Nei, 1972) are presented in Table 3. The mean values of *I* range from 0.906 in tetraploid populations of *A. media* to 0.977 in tetraploid *A. aromatica* populations (values of *D* have correspondingly low values; Table 3). The lowest value of *I* for intraspecific comparisons was 0.837 between two populations of tetraploid *A. media,* whereas the highest (0.996) were between populations of tetraploid *A. aromatica,* diploid *A. media,* and tetraploid *A. umbrinella* (Table 3). The pooled diploid populations have an average *I* of 0.898 and the polyploids have $I = 0.927$ (Table 3).

Interpopulational interspecific comparisons of all populations for *I* and *D* produce a matrix that is too large to reproduce here, but a cluster analysis of the distance matrix effectively reduces these data. A phenogram (Fig. 3) was extracted from a UPGMA cluster analysis of the matrix of *D* values derived from all pairwise combinations of 44 populations. Inspection of the phenogram reveals weak patterns with slight amounts of clustering within taxa or the cytological subdivisions of taxa. The diploid *A. media* (*A. pulchella*) form a cohesive unit with two tetraploid *A. media* populations interspersed. These two tetraploid *A. media* (M7 and M11) are populations that are monomorphic for *Tpi-1*^{b}, an allele that is otherwise exclusive to the six populations of diploid *A. media.* Four other populations of tetraploid *A. media* (M10, M18, M14, M13) also possess the *Tpi-1*^{b} allele, but these are not closely associated with the others in the phenogram. Populations of two other diploids, *A. aromatica* and *A. umbrinella,* are not clustered together and each of them is more similar to a population of another species or tetraploid population of the same species (Fig. 3). The population of *A. densifolia* is most similar to a tetraploid population of *A. umbrinella* (Fig. 3). The tetraploid *A. aromatica* populations form a fairly close association including one of the diploid populations of *A. aromatica* (A1). Tetraploid populations of *A. media* and *A. umbrinella* are aggregated into a few clusters of populations (Fig. 3). Two populations (U17 and U18) of *A. umbrinella* are morphologically atypical in that they appear to be intermediate between *A. umbrinella* and *A. microphylla* (U18) or *A. media* (U17), and are most closely linked with *A. umbrinella* (Fig. 3). In two instances, three populations were obtained from the same mountain slope, but were not closely associated in the cluster analysis (Fig. 3). For example, populations of *A. aromatica* (A2), *A. media* (M9) and *A. umbrinella* (U8) occur at different elevations on the east slope of Mt. Sacajawea (Bridger Range, Montana), but in the cluster analysis (Fig. 3) they are not tightly clustered, indicating they are distinct entities with respect to both morphology and allozyme variation.

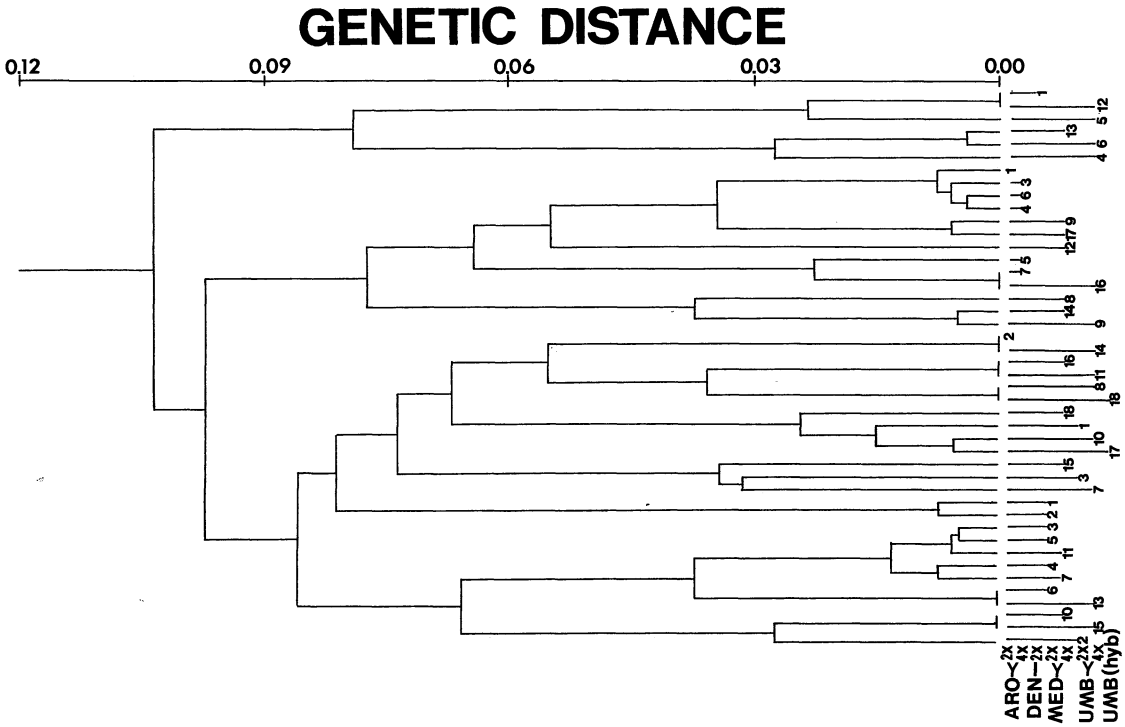

Fig. 3. Distance phenogram (UPGMA) derived from Nei's standard genetic distances of all pairwise comparisons of 44 populations from among *A. aromatica, A. densifolia, A. media* sensu lato, and *A. umbrinella.* Populations from each taxon are labeled with the first three letters of their specific epithets. Two morphologically atypical populations of *A. umbrinella* are labeled as UMB (hyb). Ploidy levels are indicated as diploid (2*x*) or tetraploid (4*x*). Population designations within each taxon are the same as those given in the Appendix. Cophenetic correlation coefficient is 0.8489.

Genetic identities and distances among the taxa (Table 4) indicate that the four taxa and their cytological subdivisions have diverged only slightly from one another, with *A. densifolia* diverging the most (Table 4). When the matrix of genetic distances is clustered (UPGMA) the resulting phenogram (Fig. 4) graphically portrays the divergence between *A. densifolia* and the remaining taxa. Interestingly, diploid and tetraploid cytotypes within each taxon are always most closely linked (Fig. 4).

DISCUSSION—*Morphological differentiation*—The morphological variation in this group has been assessed by numerical taxonomic techniques (Bayer, 1987b). The study included diploids and polyploids of *A. aromatica, A. media,* and *A. umbrinella. Antennaria densifolia* was not included in that analysis (Bayer, 1987b) because it was thought to be a primarily subarctic species with a distinct morphology from the other taxa. *Antennaria densifolia* is most similar to *A. aromatica,* both with respect to morphology and habitat, although because only one population of *A. densifolia* is known in detail it is difficult to make meaningful comparisons. The population of *A. densifolia* from Montana is high alpine, while *A. aromatica* occurs from just below treeline to low alpine. Both species occur on talus that is usually of limestone formation. *Antennaria aromatica* has glandular hairs over the entire plant, which produce a citronellalike odor when crushed, but *A. densifolia* lacks these features. *Antennaria densifolia* produces flags (a flat, scarious tip; accorded taxonomic importance and characteristic of many *Antennaria*) at the end of all upper cauline leaves, but *A. aromatica* lacks these. The leaves of *A. densifolia* are small, very densely packed and canescent, whereas those of *A. aromatica* are relatively larger, loosely arranged and lanate.

Antennaria media sensu lato and *A. umbrinella* have diverged morphologically from *A. aromatica* (Bayer, 1987b) and *A. densifolia,* but they are not always morphologically differentiated from each other. The diploid cytotypes of *A. media* and *A. umbrinella* are morphologically distinct and have widely disjunct ranges (Bayer and Stebbins, 1987). *Antennaria pulchella* (diploid *A. media*) occurs in the alpine of the Sierra Nevada Mountains and the

adjacent Carson Range of Nevada (Fig. 2). The diploid cytotypes of *A. umbrinella* occur at lower montane elevations in the Rocky Mountains of Montana, Wyoming, and Idaho (Fig. 1) and have not been recognized as a species distinct from the tetraploid cytotype mainly because they are difficult to separate reliably.

Morphological intergradation has been noted between the tetraploid cytotypes of *A. media* and *A. umbrinella,* which have overlapping ranges and habitats. Clinal morphological variation has been noted, especially in the Rocky Mountains where polyploid *A. media* is sympatric with both diploid and polyploid *A. umbrinella* (Fig. 1, 2). In the Wind River Range of west-central Wyoming, *A. umbrinella* (*WY-501*; U12) occurs at 2,895 m, *A. media-A. umbrinella* intermediates (*WY-502*; U17) occur at 2,987 m, and *A. media* (*WY-503*; M16) is alpine at 3,290 m. Clinal variation in morphology exists on this slope (Blue Ridge below Cony Mountain) ranging from typical *A. umbrinella* to typical *A. media* over a 395 m change in elevation (Appendix). Additionally, occasional intermediates between *A. aromatica* and *A. media* have been detected; see specimens from Gunnison Co., Colorado, Bayer et al. *CO-435, CO-441, CO-449* in ALTA and RM.

Morphological evidence suggests that four distinct diploids should be recognized, *A. aromatica, A. densifolia, A. pulchella* (diploid *A. media*), and *A. umbrinella.* The polyploids, *A. aromatica, A. densifolia, A. media* sensu stricto, and *A. umbrinella* are apparently interracial autopolyploid derivatives (see Grant, 1981, for discussion of terminology for the types of polyploids) of these diploids (Bayer, 1987b). *Antennaria media* polyploids can usually be differentiated from their diploid relatives with a reasonable degree of confidence, but *A. aromatica* and *A. umbrinella* diploids and tetraploids cannot always be reliably separated. Specific boundaries become obscure at the polyploid level apparently because some populations are segmental allopolyploids, being hybrid combinations derived from four weakly differentiated diploids.

Genetic differentiation—In general, the degree of genetic variation is low with only a moderate amount of genetic divergence among the taxa, as demonstrated by genetic statistics (Tables 1–4). The value of A for all populations is 1.36, comparable to plants reported by Hamrick, Linhart, and Mitton (1979) with similar life history traits (Table 1). P for all populations (0.23), is slightly lower than values reported for other plants with similar life histories (Table 1) (Hamrick et al., 1979). The value of H_{obs}

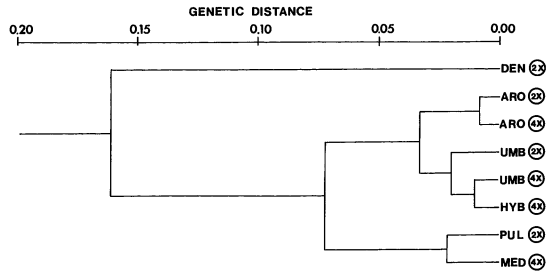

Fig. 4. Distance phenogram (UPGMA) derived from Nei's standard genetic distances of all pairwise comparisons of 8 groups of *Antennaria. Antennaria aromatica* (diploid and tetraploid), *A. densifolia* (diploid), *A. media* (tetraploid), *A. pulchella* (diploid), and *A. umbrinella* (diploid and tetraploid) are labeled with the first three letters of their specific epithets. Morphologically atypical populations of *A. umbrinella,* discussed in the text, are labeled as HYB. Ploidy levels are indicated as diploid ($2x$) or tetraploid ($4x$). Cophenetic correlation coefficient is 0.9267.

(average observed heterozygosity) of 0.118 for all populations is somewhat lower than values reported by Hamrick et al. (1979). This value for diploids (0.073) is significantly different ($P = 0.0004$) from that of polyploids (0.135), suggesting that the average polyploid is more heterozygous than the average diploid. Values of H_{obs} for diploid populations are not significantly different from expected values (H_{exp}) indicating that such populations are in Hardy-Weinberg equilibrium (Table 1).

Nei's gene diversity statistics (Nei, 1973) reveal additional information regarding genetic structure of *Antennaria* populations. Tetraploid populations of *A. umbrinella* have the highest total diversity at 0.142, while the lowest diversity was in the diploid population of *A. densifolia* (0.022; Table 2). The more narrowly distributed taxa *A. densifolia* ($2x$), *A. aromatica* ($2x$), *A. aromatica* ($4x$), *A. pulchella* ($2x$), and *A. umbrinella* ($2x$) have lower values of H_T, than the two widely distributed polyploids *A. media* ($4x$) and *A. umbrinella* ($4x$) (Table 2). This is compatible with the hypothesized pattern (Stebbins, 1942; Babbel and Selander, 1974), in which more narrow endemic species have less genetic variability than widely distributed ones (niche width-variation hypothesis). Loveless and Hamrick (1984) have pointed out that the niche-width variation hypothesis has rarely been substantiated for plants. Inspection of values of H_S, D_{ST}, and G_{ST} (Table 2) for all loci indicates that variation within taxa is sequestered primarily within populations and not between them, as is especially evidenced by relatively low values of G_{ST}. Values of G_{ST} for individual loci under the category

TABLE 4. *Nei's genetic distances (lower triangle) and genetic identities (upper triangle) for all pairwise comparisons of populations within 7 groups of* Antennaria

Taxa	AROM (2x)	AROM (4x)	DENS (2x)	MEDI (2x)	MEDI (4x)	UMBR (2x)	UMBR (4x)
A. aromatica (2x)		0.992	0.842	0.912	0.954	0.961	0.969
A. aromatica (4x)	0.008		0.851	0.916	0.957	0.970	0.963
A. densifolia (2x)	0.172	0.162		0.870	0.896	0.838	0.862
A. media (2x)	0.092	0.087	0.139		0.979	0.903	0.915
A. media (4x)	0.047	0.044	0.110	0.021		0.954	0.959
A. umbrinella (2x)	0.040	0.031	0.177	0.102	0.047		0.981
A. umbrinella (4x)	0.032	0.038	0.149	0.089	0.042	0.019	

of "all taxa" (Table 2) indicate that interspecific population divergences have occurred primarily at *Lap-1, Tpi-3, Acp-1, Lap-2,* and *Skdh-1.* Loveless and Hamrick (1984) have summarized gene diversity statistics for plants for various ecological and life history categories. In comparison with other outcrossing (dioecious), sexual, insect pollinated, long-lived perennials, the figures for H_T, H_S, D_{ST}, and G_{ST} (Table 2) are lower than values cited by Loveless and Hamrick (1984), except tetraploid *A. media* and tetraploid *A. umbrinella* where figures equal or surpass their values.

The values of *A, P,* H_{obs} (Table 1), and gene diversity statistics (Table 2), are very similar to values presented in previous studies of other sexual species of *Antennaria* (*A. neglecta* Greene, *A. plantaginifolia* (L.) Hook., *A. racemosa* Hook., *A. solitaria* Rydb., and *A. virginica* Stebb. (Bayer and Crawford, 1986) as well as *A. corymbosa* E. Nels., *A. marginata* Greene, *A. microphylla* Rydb., and *A. rosulata* Rydb. (Bayer, 1988)).

The interspecific differences among taxa are due primarily to diverse allelic frequencies at individual loci among the taxa, *not* to the presence of unique alleles in the taxa. The values of *I* and *D* are within the scope of values for intraspecific population comparisons found in other perennial herbs (see Gottlieb, 1981a; Crawford, 1983) and other *Antennaria* species (Bayer and Crawford, 1986; Bayer, 1988). This indicates a high degree of genetic similarity among populations within each of the taxa and cytological subdivisions within the taxa.

The values of *I* and *D* (Table 4) are higher and lower, respectively, than most interspecific comparisons previously reported for other congeneric groups with similar life history traits (see Crawford, 1983). The values of *I* are slightly higher than those for western North American species of *Antennaria* from section *Dioicae* (viz. *A. corymbosa, A. marginata, A. microphylla,* and *A. rosulata*; Bayer, 1988), than those for primarily eastern North American *Dioicae* (viz. *A. neglecta* and *A. virginica*; Bayer and Crawford, 1986) and for North American *Antennaria* in section *Plantaginifoliae* (viz. *A. plantaginifolia, A. racemosa,* and *A. solitaria*; Bayer and Crawford, 1986).

A question that needs to be addressed is: What are the genetic consequences of polyploidy in *Antennaria*? A direct comparison of the genetic structure of diploids and polyploids reveals the similarities and differences between the two groups. Polyploids maintain the same alleles found in their diploid progenitors, i.e., no allele present in a diploid was absent from its polyploid derivatives and vice versa. Tetrasomic inheritance is inferred in the polyploids because 1) unbalanced heterozygotes are often observed and 2) some plants maintain three alleles at a locus. Direct genetic demonstration of tetrasomic inheritance is forthcoming through observation of segregation ratios from controlled crosses. Evidence of fixed heterozygosity, as might be expected if these polyploids were strict allopolyploids (Soltis and Rieseberg, 1986), was not observed at any locus in any of the sexual polyploid populations. Similar observations were noted in diploid and tetraploid cytotypes of the Appalachian shale barren endemic, *A. virginica* (Bayer and Crawford, 1986). *T* tests indicate that values of *A, P,* H_{obs} (Table 1) for pooled diploids and pooled polyploids are only significantly different with respect to H_{obs} suggesting that the level of heterozygosity is higher in polyploids than in diploids. These genetic data from *Antennaria* are similar to those found by Soltis and Rieseberg (1986) in autopolyploid *Tolmiea menziesii* (Saxifragaceae) or Crawford and Smith (1984) in autohexaploid *Coreopsis grandiflora* var. *longipes* (Asteraceae). The results from *Antennaria* differ from other enzyme electrophoretic studies of strict allopolyploids (*Tragopogon* (Asteraceae); Roose and Gottlieb, 1976 and *Asplenium* (Polypodiaceae); Werth, Guttman, and Eshbaugh, 1985) in which significant genetic divergence among the diploid species oc-

curred. The diploids in a previous study of *Antennaria* had diverged to the extent that their derivatives were regarded as [segmental] allopolyploids (Bayer and Crawford, 1986).

Speciation and taxonomy—Crawford (1985) has summarized the application of isozymes for determination of modes of speciation in plants. In the case of *Antennaria,* a mode of speciation has been hypothesized in which morphological divergence has not been accompanied by a similar level of isozyme divergence (Bayer and Crawford, 1986; Bayer, 1988). Similar patterns have been observed in several additional genera; *Tetramolopium* (Asteraceae; Lowrey and Crawford, 1985), *Bidens* (Asteraceae; Helenurm and Ganders, 1985), *Dendroseris* (Asteraceae; Crawford, Stuessy, and Silva O., 1987), *Quercus* (Fagaceae; Manos and Fairbrothers, 1987), and *Heuchera* (Saxifragaceae; Soltis, 1985).

There is some disparity between the degree of morphological and isozyme divergence in *Antennaria. Antennaria aromatica, A. densifolia, A. media* sensu lato, and *A. umbrinella* are fairly distinct morphologically, although some morphological overlap exists between tertraploid *A. aromatica, A. media,* and *A. umbrinella,* in which the majority of tetraploids appear to be interracial autopolyploid derivatives of the diploids (Bayer, 1987b). Other tetraploids are ostensibly segmental allopolyploids as they possess morphological characters that are attributable to more than one diploid. Isozyme data are supportive of this interpretation, as most tetraploid populations have highest genetic identity values with the diploid that they are inseparable from morphologically (diploid/tetraploid conspecifics). In other cases, some tetraploid morphotypes are inseparable from conspecific diploid/tetraploid cytotypes, yet have higher genetic affinities with another species. A good example of this is population M16 (tetraploid *A. media*; Appendix), which is morphologically indistinguishable from other tetraploid *A. media* yet, as evaluated by values of *I,* is more similar to a tetraploid population of *A. umbrinella* (U11; Appendix). Furthermore, diploid populations of *A. media* (= *A. pulchella*) are monomorphic for *Tpi-1*^{b}, whereas some tetraploid *A. media* are monomorphic for *Tpi-1*^{a}, an allele found in the diploids of *A. aromatica, A. densifolia,* and *A. umbrinella.* This is strong evidence for an hybrid origin (segmental allopolyploids) for certain *A. media* populations. Individuals that appear to be autopolyploids, based on morphology, may prove not to be once additional information from cytogenetics, flavonoid chemistry, and biochemical genetics are obtained.

Available evidence indicates that *A. aromatica, A. densifolia, A. media,* and *A. umbrinella* have undergone rapid evolution at the diploid level, which has involved morphological divergence, slight isozyme divergence, and adaptation to specific ecological niches in two centers of diversity, the Sierra Nevada of California and the Montana Rocky Mountains. Subsequently, polyploids have evolved from these moderately differentiated diploid species which can be categorized as occurring along a continuum from interracial autopolyploids to segmental allopolyploids. These polyploids now represent separate evolutionary lineages from their diploid progenitors.

Taxonomically, it is best to recognize diploid and tetraploid cytotypes of both *A. aromatica* and *A. umbrinella* as conspecific because their respective diploid and polyploid cytotypes are morphologically indistinguishable. *Antennaria pulchella* (diploid *A. media*) and *A. media* sensu stricto should be considered a distinct species because they are morphologically differentiable. Living material of *A. densifolia* from the subarctic needs to be obtained for comparison before a decision can be made concerning the status of diploid *A. densifolia* from Montana. The low levels of genetic divergence among morphologically distinct taxa calls for taxonomic conservatism. I oppose the view that some would advocate in recognizing many microspecies, such as *A. stolonifera* A. E. Porsild (= *A. media* sensu stricto), that are dubious on the basis of morphology and that are certainly not differentiated isozymically.

LITERATURE CITED

BABBEL, G. R., AND R. K. SELANDER. 1974. Genetic variability in edaphically restricted and widespread plant species. Evolution 28: 619–630.

BAYER, R. J. 1984. Chromosome numbers and taxonomic notes for North American species of *Antennaria* (Asteraceae: Inuleae). Syst. Bot. 9: 74–83.

———. 1987a. Evolution and phylogenetic relationships of the *Antennaria* (Asteraceae: Inuleae) polyploid agamic complexes. Biol. Zentralbl. 106: 683–698.

———. 1987b. Morphometric analysis of western North American *Antennaria* Gaertner (Asteraceae: Inuleae). I. Sexual species of sections Alpinae, Dioicae, and Plantaginifoliae. Canad. J. Bot. 65: 2389–2395.

———. 1988. Patterns of isozyme variation in western North American *Antennaria* (Asteraceae: Inuleae). I. Sexual species of section *Dioicae.* Syst. Bot. 13: 525–537.

———, AND D. J. CRAWFORD. 1986. Allozyme divergence among five diploid species of *Antennaria* (Asteraceae: Inuleae) and their allopolyploid derivatives. Amer. J. Bot. 73: 287–296.

———, AND G. L. STEBBINS. 1983. Distribution of sexual

and apomictic populations of *Antennaria parlinii*. Evolution 37: 555–561.

———, AND ———. 1987. Chromosome numbers, patterns of distribution, and apomixis in *Antennaria* (Asteraceae: Inuleae). Syst. Bot. 12: 305–319.

———, J. C. LADUKE, AND D. J. CRAWFORD. 1987. Isozyme variation in *Trillium nivale* Riddell (Liliaceae). Canad. J. Bot. 65: 2250–2254.

CARDY, B. J., C. W. STUBER, AND M. M. GOODMAN. 1981. Techniques for starch gel electrophoresis of enzymes from maize (*Zea mays* L.). Institute of Statistics Mimeograph Series No. 1317. North Carolina State University, Raleigh, NC.

CRAWFORD, D. J. 1983. Phylogenetic and systematic inferences from electrophoretic studies. *In* S. D. Tanksley and T. J. Orton [eds.], Isozymes in plant genetics and breeding, Part A. Elsevier, Amsterdam.

———. 1985. Electrophoretic data and plant speciation. Syst. Bot. 10: 405–416.

———, AND E. B. SMITH 1984. Allozyme divergence and intraspecific variation in *Coreopsis grandiflora* (Compositae). Syst. Bot. 9: 219–225.

———, T. F. STUESSY, AND M. SILVA O. 1987. Allozyme divergence and the evolution of *Dendroseris* (Compositae: Lactuceae) on the Juan Fernandez Islands. Syst. Bot. 12: 435–443.

DIXON, W. J. [ED.] 1981. BMDP statistical software. University of California Press, Berkeley.

EVERT, E. F. 1984. A new species of *Antennaria* (Asteraceae) from Montana and Wyoming. Madroño 31: 109–112.

GASTONY, G. J., AND D. C. DARROW. 1983. Chloroplastic and cytosolic isozymes of the homosporous fern *Athurium filix-femina*. Amer. J. Bot. 70: 1409–1415.

GOTTLIEB, L. D. 1981a. Electrophoretic evidence and plant populations. Progr. Phytochem. 7: 1–46.

———. 1981b. Gene number in species of Asteraceae that have different chromosome number. Proc. Natl. Acad. Sci. USA 78: 3726–3729.

GRANT, V. 1981. Plant speciation, 2d ed. Columbia, New York.

HAMRICK, J. L., Y. B. LINHART, AND J. B. MITTON. 1979. Relationships between life history characteristics and electrophoretically detectable genetic variation in plants. Annual Rev. Ecol. Syst. 10: 173–200.

HARTL, D. 1980. Principles of population genetics. Sinauer, Sunderland, MA.

HELENURM, K., AND F. R. GANDERS. 1985. Adaptive radiation and genetic differentiation in Hawaiian *Bidens*. Evolution 39: 753–765.

LOVELESS, M. D., AND J. L. HAMRICK. 1984. Ecological determinants of genetic structure in plant populations. Annual Rev. Ecol. Syst. 15: 65–95.

LOWREY, T. K., AND D. J. CRAWFORD. 1985. Allozyme divergence and evolution in *Tetramolopium* (Compositae: Astereae). Syst. Bot. 10: 64–72.

MANOS, P. S., AND D. E. FAIRBROTHERS. 1987. Allozymic variation in populations of six northeastern American red oaks (Fagaceae: *Quercus* subg. *Erythrobalanus*). Syst. Bot. 12: 365–373.

NEI, M. 1972. Genetic distance between populations. Amer. Naturalist 106: 283–292.

———. 1973. Analysis of gene diversity in subdivided populations. Proc. Nat. Acad. Sci. USA 70: 3321–3323.

PORSILD, A. E. 1945. The alpine flora of the east slope of the Mackenzie mountains, Northwest Territories. Natl. Mus. Canada Biol. Ser. 30: 1–35.

ROHLF, F. J. 1987. NTSYS-pc: numerical taxonomy and multivariate analysis system for the IBM PC microcomputer (and compatibles). Applied Biostatistics, Setauket, NY.

ROOSE, M. L., AND L. D. GOTTLIEB. 1976. Genetic and biochemical consequences of polyploidy in *Tragopogon*. Evolution 30: 818–830.

RUTTER, N. W. 1984. Pleistocene history of the western Canadian ice-free corridor. *In* Quarternary stratigraphy of Canada—a Canadian contribution to IGCP project 24. Geological Survey of Canada paper 84-10, Ottawa.

SNEATH, P. H. A., AND R. R. SOKAL. 1973. Numerical taxonomy. W. H. Freeman, San Francisco.

SOLTIS, D. E. 1985. Allozymic differentiation among *Heuchera americana, H. parviflora, H. pubescens,* and *H. villosa* (Saxifragaceae). Syst. Bot. 10: 193–198.

———, C. H. HAUFLER, D. C. DARROW, AND G. H. GASTONY. 1983. Starch gel electrophoresis of ferns: a compilation of grinding buffers, gel and electrode buffers, and staining schedules. Amer. Fern J. 73: 9–27.

———, AND L. H. RIESEBERG. 1986. Autopolyploidy in *Tolmiea menziesii* (Saxifragaceae): genetic insights from enzyme electrophoresis. Amer. J. Bot. 73: 310–318.

STEBBINS, G. L. 1942. The genetic approach to problems of rare and endemic species. Madroño 6: 241–258.

WEEDEN, N. F., AND L. D. GOTTLIEB. 1980a. Isolation of cytoplasmic enzymes from pollen. Pl. Physiol. 66: 400–403.

———, AND ———. 1980b. The genetics of chloroplast enzymes. J. Hered. 71: 392–396.

WERTH, C. R., S. I. GUTTMAN, AND W. H. ESHBAUGH. 1985. Electrophoretic evidence of reticulate evolution in the Appalachian *Asplenium* complex. Syst. Bot. 10: 184–192.

WHITKUS, R. 1985. FORTRAN program for computing genetic statistics from allelic frequency data. J. Hered. 76: 142.

APPENDIX. *Locality data for 44 populations of* Antennaria aromatica, A. densifolia, A. media, *and* A. umbrinella. *Presented are taxon names, population designations, state, county, latitude, longitude, elevation (meters) above sea level, collectors and collection number and reproductive mode (S = sexual; A = asexual). All populations have been determined as diploid (2n = 28) or tetraploid (2n = 56). Voucher specimens are at ALTA*

Taxa/populations/provenance			Lat.	Long.	Elev.	Collectors/vouchers/repro. mode
A. aromatica (diploids)						
A1	MT	Carbon	45°03′	109°25′	2,972	*Bayer and Lebedyk MT-500* (S)
A2	MT	Gallatin	45°54′	110°58′	2,515	*Bayer, Joncas, and Lebedyk MT-628* (S)
A. aromatica (tetraploids)						
A3	MT	Cascade	47°08′	111°03′	2,134	*Bayer, DeLuca, and Lebedyk MT-747* (S)
A4	MT	Judith Basin	46°50′	110°43′	2,426	*Bayer, DeLuca, and Lebedyk MT-754* (S)
A5	MT	Madison	44°59′	111°50′	2,899	*Bayer, Joncas, and Lebedyk MT-634* (S)
A6	MT	Teton	47°55′	112°43′	2,057	*Bayer, DeLuca, and Lebedyk MT-768* (S)
A7	WY	Park	44°57′	109°38′	3,048	*Bayer, Joncas, and Lebedyk WY-626* (A)
A. densifolia (diploid)						
D1	MT	Granite	46°03′	113°17′	2,789	*Bayer, DeLuca, and Lebedyk MT-725* (S)
A. media (= *A. pulchella*) (diploid)						
M1	CA	Inyo	36°29′	118°13′	3,230	*Bayer, DeLuca, and Lebedyk CA-700* (S)
M2	CA	Inyo	37°08′	118°34′	3,237	*Bayer, DeLuca, and Lebedyk CA-732* (S)
M3	CA	Inyo	36°45′	118°22′	3,225	*Bayer, DeLuca, and Lebedyk CA-707* (S)
M4	CA	Inyo	37°11′	118°38′	3,170	*Bayer, DeLuca, and Lebedyk CA-724* (S)
M5	CA	Mono	37°54′	119°18′	3,078	*Bayer, DeLuca, and Lebedyk CA-720* (S)
M6	NV	Washoe	39°20′	119°56′	3,288	*Stebbins NV-601* (S)
A. media (tetraploids)						
M7	ID	Custer	44°35′	114°28′	2,804	*Bayer, Joncas, and Lebedyk ID-604* (A)
M8	MT	Deerlodge	46°03′	113°16′	2,804	*Bayer and Lebedyk MT-519* (A)
M9	MT	Gallatin	45°54′	110°58′	2,484	*Bayer, Joncas, and Lebedyk MT-629* (A)
M10	MT	Glacier	48°40′	113°43′	2,073	*Bayer and Lebedyk MT-545* (A)
M11	MT	Ravalli	46°09′	114°30′	2,377	*Bayer, Joncas, and Lebedyk MT-605* (A)
M12	OR	Deschutes	42°55′	122°03′	2,721	*Stebbins OR-511* (A)
M13	OR	Klamath	43°54′	121°50′	1,676	*Stebbins OR-506* (S)
M14	UT	Summit	40°43′	110°53′	3,413	*Bayer, Joncas, and Lebedyk UT-616* (A)
M15	WY	Big Horn	44°17′	107°09′	2,957	*Bayer, Joncas, and Lebedyk WY-636* (A)
M16	WY	Fremont	42°38′	108°55′	3,290	*Bayer and Lebedyk WY-503* (A)
M17	WY	Park	44°58′	109°27′	3,200	*Bayer, Joncas, and Lebedyk WY-621* (A)
M18	WY	Sublette	43°17′	109°52′	2,685	*Bayer, Joncas, and Lebedyk WY-616* (S)
A. umbrinella (diploids)						
U1	MT	Gallatin	45°05′	111°12′	2,073	*Bayer, Joncas, and Lebedyk MT-630* (S)
U2	MT	Ravalli	45°45′	114°26′	1,615	*Bayer, Joncas, and Lebedyk MT-600* (S)
A. umbrinella (tetraploids)						
U3	WY	Yellowstone Park	44°53′	110°44′	2,243	*Bayer and Lebedyk WY-513* (S)
U4	CO	Jackson	40°55′	106°19′	2,408	*Bayer and Lebedyk CO-527* (S)
U5	ID	Custer	44°12′	113°50′	2,535	*Bayer, Joncas, and Lebedyk ID-601* (S)
U6	MT	Beaverhead	45°18′	112°55′	1,951	*Bayer and Lebedyk MT-506* (S)
U7	MT	Deerlodge	46°04′	113°16′	2,499	*Bayer and Lebedyk MT-511* (S)
U8	MT	Gallatin	45°55′	110°54′	1,980	*Bayer and Lebedyk MT-503* (S)
U9	MT	Granite	46°26′	113°41′	1,402	*Bayer and Lebedyk MT-529* (S)
U10	MT	Madison	44°56′	111°50′	2,896	*Bayer, Joncas, and Lebedyk MT-632* (S)
U11	WY	Big Horn	44°48′	107°54′	2,591	*Bayer and Lebedyk WY-517* (S)
U12	WY	Fremont	42°38′	108°55′	2,895	*Bayer and Lebedyk WY-501* (S)
U13	WY	Johnson	44°09′	107°04′	2,944	*Bayer, Joncas, and Lebedyk WY-632* (S)
U14	WY	Johnson	44°19′	106°57′	2,438	*Bayer, Joncas, and Lebedyk WY-634* (S)
U15	WY	Sublette	43°17′	109°52′	2,438	*Bayer, Joncas, and Lebedyk WY-604* (S)
U16	WY	Sublette	43°15′	109°45′	2,326	*Bayer, Joncas, and Lebedyk WY-601* (S)
U17	WY	Fremont	42°38′	108°55′	2,987	*Bayer and Lebedyk WY-502* (S)
U18	WY	Sublette	43°15′	109°45′	2,325	*Bayer, Joncas, and Lebedyk WY-602* (S)