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Patterns of Isozyme Variation in the *Antennaria rosea* (Asteraceae: Inuleae) Polyploid Agamic Complex

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ABSTRACT. *Antennaria* is a genus of dioecious, perennial herbs, which are distributed over much of North America and Eurasia. The *A. rosea* polyploid agamic complex occurs throughout western North America and is perhaps the most complicated, with respect to morphology and taxonomy, of all the *Antennaria* species complexes. The complex is composed of gametophytic apomicts and consequently the populations contain only pistillate clones. Morphological studies have demonstrated that the *A. rosea* complex is a compilospecies derived through hybridization from perhaps as many as eight, sexually reproducing species of *Antennaria*, with which it has a partially sympatric distribution. Enzyme electrophoresis was used both to assess the degree of divergence among 33 populations of *A. rosea*, as well as to determine the amount of divergence between *A. rosea* and its sexual progenitors. Gene statistics demonstrate that *A. rosea* contains more gene diversity than its amphimictic relatives. The electrophoretic data provide evidence, independent, yet supportive, of morphology, that *A. corymbosa*, *A. microphylla*, and *A. umbrinella* are among the sexual progenitors of some of the *A. rosea* segregates. Morphology also implicates *A. aromatica*, *A. densifolia*, *A. marginata*, *A. media*, *A. racemosa*, and *A. rosulata* in the parentage of *A. rosea*, although the electrophoretic data neither support nor contradict this hypothesis independent of morphology. The *A. rosea* complex is probably of recent origin because it has diverged only moderately from its sexual progenitors, having only one novel allele that does not occur in the amphimicts.

Antennaria rosea E. Greene is one of the most morphologically diverse polyploid complexes in *Antennaria* Gaertner. The center of diversity for *A. rosea* is the Rocky Mountains of western North America and its range stretches from New Mexico and southern California, north to Alaska and the Northwest Territories, and east through Alberta and Saskatchewan to the western shores of Hudson Bay. It also occurs as disjunct populations around the shore of James Bay, the north shore of Lake Superior, the Gaspé Peninsula in eastern Quebec, and in western Newfoundland. It occurs in a broad scope of habitats from dry sagebrush steppe to moist alpine tundra.

The species has triploid ($2n = 42$), tetraploid ($2n = 56$), and pentaploid ($2n = 70$) cytotypes, but the tetraploids are the most prevalent (Bayer and Stebbins 1987). *Antennaria rosea* is a gametophytic apomict, and because the genus is dioecious, populations of *A. rosea* consist entirely of pistillate clones (Bayer 1987a; Bayer and Stebbins 1987). Taxonomically, I have treated this compilospecies as a large polymorphic species, *A. rosea* s.l., because it is impractical to try to recognize all the microspecies that delineate the complex (Bayer, in press c). In giving taxonomic recognition to all the microspecies from northwestern Canada belonging to this complex, Chmielewski and Chinnappa (1988) have advocated the opposite approach. I regard this concept of extreme taxonomic splitting in the *A. rosea* complex as unusable.

The variation in the *A. rosea* complex is derived from several sexually reproducing species of *Antennaria*, and morphological studies have revealed that the complex is related to those species that occur primarily in the southern, unglaciated, portions of the western cordillera (Bayer, in press a). *Antennaria aromatica* Evert, *A. corymbosa* E. Nelson, *A. media* E. Greene, *A. microphylla* Rydb., *A. racemosa* Hook., and *A. umbrinella* Rydb. are sexual species that appear to be involved in the parentage of *A. rosea*. Additionally, *A. densifolia* A. Pors., *A. marginata* E. Greene, and *A. rosulata* Rydb. may have contributed to the genetic composition of the *A. rosea* complex. *Antennaria aromatica*, *A. corymbosa*, *A. racemosa*, and *A. umbrinella* occur primarily in the unglaciated portions of the northern Rocky Mountains, whereas *A. marginata* and *A. rosulata* occur in the southern Rocky Mountains, mainly north of Mexico. Two of the sexual species, *A. microphylla* and *A. media*, are more widespread throughout the western Cordillera from the southern portions in New Mexico and

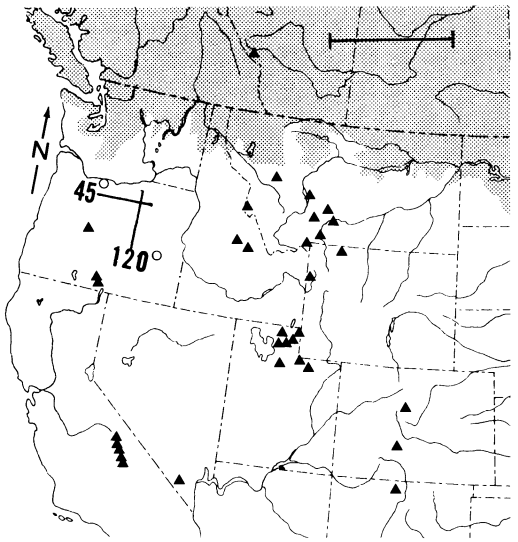

FIG. 1. Locations of 33 sampled populations of *Antennaria rosea* (solid triangle). Maximum extent of Wisconsin Glaciation is indicated by stippling. Bar equals 500 km.

California to the Yukon. *Antennaria densifolia* occurs chiefly in the Northwest Territories and Yukon, with a single disjunct population in Montana. The ranges of the sexual species, for the most part, overlap completely with that of *A. rosea*. Maps outlining the distributions of these sexual species along with the populations that were surveyed electrophoretically can be found in Bayer (1988) and Bayer (in press b). Suites of morphological characters that are unique to a particular sexual species often occur in different combinations in the segregates of *A. rosea* (Bayer, in press a). Consequently, *A. rosea* is a compilospecies, having arisen through multiple hybridization and introgression from among several sexual species.

The degree of morphological divergence among the sexual species related to *A. rosea* has been assessed (Bayer 1987b) and the purpose of this paper is to determine the degree of genetic divergence at loci encoding soluble enzymes both among populations of *A. rosea* and between populations of *A. rosea* and its sexual progenitors. An additional goal of this analysis was to examine the relationships of populations of *A. rosea* with its presumed progenitors.

MATERIALS AND METHODS

Populations of *A. rosea* were sampled from a major portion of the principal range of the species (fig. 1) in western North America. Population samples of the Atlantic North American disjuncts were unavailable for analysis. A total of 604 plants were assayed from 33 populations (table 1). Plants were collected from populations by removing ramets in the field and placing them in cultivation in the phytotron of the University of Alberta. The chromosome number of each collection was obtained using the methods of Bayer (1984) and these are reported in table 1. Generally, young leaves were used as sources of enzymes, but young flowering heads, which possess the highest enzyme activity, were used when available. Electrophoretic methodologies, including buffer systems and staining schedules, are identical to those cited in Bayer (1988).

The enzyme systems resolved and the number of putative loci scored (in parentheses) are as follows: Acid phosphatase—ACP (1), glutamate dehydrogenase—GDH (1), general protein—GP (1), leucine aminopeptidase—LAP (2),

TABLE 1. Locality data for 33 populations of *Antennaria rosea*. Presented are state/province, county, and collection numbers. Population designations, referred to in the text, are in parentheses following the collection numbers. All populations have been determined as tetraploid ($2n = 56$), except those marked by an asterisk, which are triploid ($2n = 42$). Voucher specimens are at ALTA.

CANADA. **Alberta:** Kananaskis Valley, *Bayer et al. AB-700* (R1). U.S.A. **California:** Inyo Co., *Bayer et al. CA-704* (R2); *Bayer et al. CA-729* (R3); *Bayer et al. CA-701* (R4); *Bayer et al. CA-708* (R5); *Bayer et al. CA-733* (R6). **Colorado:** Saguache Co., *Bayer et al. CO-417* (R7); Summit Co., *Bayer et al. CO-456* (R8). **Idaho:** Custer Co., *Bayer et al. ID-602* (R9); *Bayer et al. ID-603* (R10). **Montana:** Broadwater Co., *Bayer et al. M-612* (R11); Gallatin Co., *Bayer et al. M-631* (R12); *Bayer et al. MT-701* (R13); Park Co., *Bayer et al. M-614* (R14); *Bayer et al. M-639* (R15); Powell Co., *Bayer et al. M-607** (R16); Ravalli Co., *Bayer et al. M-604* (R17); Sweetgrass Co., *Bayer et al. M-636** (R18). **Nevada:** Clark Co., *Bayer et al. NV-701* (R19). **New Mexico:** Rio Arriba Co., *Bayer & Lebedyk NM-507* (R20). **Oregon:** Deschutes Co., *Stebbins O-510* (R21); Klamath Co., *Stebbins O-609* (R22); *Stebbins O-613* (R23). **Utah:** Cache Co., *Bayer et al. UT-609* (R24); Duchesne Co., *Bayer et al. UT-618* (R25); Rich Co., *Bayer et al. UT-606B* (R26); *Bayer et al. UT-611* (R27); *Bayer et al. UT-610** (R28); Salt Lake Co., *Bayer et al. UT-603* (R29); Summit Co., *Bayer et al. UT-615* (R30); Weber Co., *Bayer et al. UT-606* (R31). **Wyoming:** Park Co., *Bayer et al. WY-629** (R32); Teton Co., *Bayer et al. WY-620* (R33).

malate dehydrogenase—MDH (4), phosphoglucoisomerase—PGI (3), phosphoglucomutase—PGM (1), shikimate dehydrogenase—SKDH (1), superoxide dismutase—SOD (2), and triosephosphate isomerase—TPI (3). Isozyme designations, in which the most anodally migrating isozyme is designated as 1, etc., are the same as those used in previous studies of *Antennaria* (Bayer 1988; Bayer, in press b; Bayer and Crawford 1986). The most anodally migrating allozyme of a given isozyme was designated as a, the next b, and so on, and they correspond to the designations used for allozymes in the related sexual species of *Antennaria* (Bayer 1988; Bayer, in press b).

The genetic bases of the enzyme banding patterns were inferred using several lines of evidence. Segregation patterns observed from populations of the presumed sexual progenitors of *A. rosea* provide insight into the genetic basis for variation seen for each enzyme. These interpretations are facilitated by knowledge of the established subunit composition of each active enzyme (Gottlieb 1982). Progeny from individual plants of *A. umbrinella*, used to determine outcrossing rates, show similar segregation patterns (Bayer, unpubl. data). Additionally, determination of the subcellular localization of the enzymes (i.e., chloroplast or cytosol) is valuable for interpretation of the gels (Bayer 1988; Bayer and Crawford 1986).

The presence of unbalanced heterozygotes in *A. rosea*, as is evidenced by unequal staining intensity in the gels, is indicative of trisomic (in triploids) and tetrasomic (in tetraploids) modes of inheritance. Also, the presence of three alleles at some loci in *A. rosea* is highly suggestive of multisomic inheritance (Soltis and Rieseberg 1986). Tetrasomic inheritance has been inferred for several other polyploid species of *Antennaria* (Bayer, in press b; Bayer and Crawford 1986). Although trisomic and tetrasomic inheritance can never be genetically proven in *A. rosea* because they are gametophytic apomicts, crosses are underway to confirm tetrasomic inheritance in sexual *A. aromatica* and *A. umbrinella*. Loci were scored based on the assumption of trisomic inheritance for triploid populations and tetrasomic for tetraploids.

The genetic data were appraised using several statistics, including mean number of alleles per locus (A), proportion of loci polymorphic (P), and observed average heterozygosity (H_{obs}). Expected average heterozygosity (H_{exp}) could not be evaluated because these polyploid asexual plants violate basic assumptions of the Hardy-Weinberg Law. Total gene diversity (H_T), intrapopulational gene diversity (H_S), interpopulational gene diversity (D_{ST}), and the coefficient of gene differentiation (G_{ST}), where $H_T = H_S + D_{ST}$, and $G_{ST} = D_{ST}/H_T$, were calculated according to the methods of Nei (1973). T-tests were used to compare A, P, H_{obs}, H_T, H_S, D_{ST}, and G_{ST} between values for *A. rosea* from this study and values from sexual species of *Antennaria* from previous studies (Bayer 1988; Bayer and Crawford 1986). Similarly, Nei's (1972) standard genetic distances (D) and genetic identities (I) were computed by the GENESTAT program (Whitkus 1985). The SAHN and TREE subroutines of the NT-SYS statistical program (pc version, Rohlf 1987) were used to generate a phenogram by the unweighted pair-group method (UPGMA; Sneath and Sokal 1973) utilizing the D matrix.

Results

The 10 enzyme systems used in this study were interpreted as being encoded by a total of 19 presumed loci. The isozymes and their allozymes (parentheses) are: ACP-1-(A to C), GDH-1-(A and B), GP-1-(A), LAP-1-(A to F), LAP-2-(A to C), MDH-1-(A), MDH-2-(A), MDH-3-(A), MDH-4-(A), PGI-1-(A), PGI-2-(A), PGI-3-(A to E), PGM-1-(A and B), SKDH-1-(A to C), SOD-1-(A), SOD-2-(A), TPI-1-(A), TPI-2-(A), and TPI-3-(A to F). A table of allelic frequencies is available from the author upon request.

General protein activity consists of a single, uniform, monomorphic band both in *A. rosea* and related sexual species and is interpreted as being encoded by a single monomorphic locus. Additional putative loci were occasionally visualized on the ACP gels, but were not scored due to unsatisfactory resolution or activity. In addition to the one locus that was scored, two additional presumed loci occur for PGM (possibly the result of a duplication), but as has been noted previously (Bayer 1988), interpretation of these isozymes is confounded by their apparent overlap. The number of isozymes present in each enzyme system is similar to those established for diploid plants for ACP (3, but only 1 scored), GDH (1), MDH (4), SKDH (1), and SOD (2) (Crawford 1983; Gottlieb 1982). As has been reported in previous studies (Bayer 1988; Bayer, in press b; Bayer and Crawford 1986), there appears to be a gene duplication in the chloroplast

forms of PGI and TPI. In PGI, a consistent 3-banded pattern is interpreted as two monomorphic, isozymic homodimers (PGI-1 and PGI-2) and the interlocus heterodimer. Lack of variation at these putative loci precludes formal genetic analysis of this situation. Similarly in TPI, a consistent 3-banded pattern is indicative of enzymes encoded by 2 loci (TPI-1 and TPI-2). *Tpi-1* is invariant, but recently, variation at *Tpi-2* has been found in *A. corymbosa* and *A. media*, which will allow confirmation of the genetic basis of these enzyme patterns. The putative PGI and TPI duplications occur in all species of *Antennaria* that have been investigated (Bayer 1988).

Pollen leachates and chloroplast extracts were used to determine the subcellular localization of isozymes, i.e., which isozymes were localized in the cytosol and which were restricted to the chloroplasts. Results from these studies indicate that the cytosolic isozymes are PGI-3, PGM-2/PGM-3 (neither scored), TPI-3, whereas the chloroplastic isozymes are PGI-1/PGI-2, PGM-1, and TPI-1/TPI-2.

The segregates of *A. rosea* contain the same allelic variants that are contained in the sexual species. The amphimicts have not diverged from one another to the extent that they each contain unique alleles at the loci surveyed. [For a complete discussion of the isozyme variation in the sexual species, including *A. aromatica*, *A. corymbosa*, *A. densifolia*, *A. marginata*, *A. media*, *A. microphylla*, *A. rosulata*, and *A. umbrinella*, consult Bayer (1988) and Bayer (in press b).] The sexual species themselves differ primarily by divergent allelic frequencies at the loci, but in some instances unique alleles do occur and these diagnostic alleles appear in the polyploid *A. rosea* segregates. *Lap-1*^{a} is contained in *A. umbrinella* and *A. rosea*, whereas *Pgi-3*^{a} is fixed in *A. microphylla* and is also found in many *A. rosea* segregates. Only *A. corymbosa* and *A. rosea* have *Gdh-1*^{b}. Several alleles occur in the sexual taxa that were not encountered in the *A. rosea* segregates; *Tpi-1*^{b} occurs exclusively in *A. corymbosa* and *A. media* (Bayer, in press b), and *Lap-2*^{d} and *Lap-2*^{e} are present in most sexual species. Only one allele, *Pgm-1*^{a}, is found in *A. rosea*, but has not been detected in the sexual species surveyed (Bayer 1988; Bayer, in press b). Unique alleles that occur in *A. corymbosa*, *A. microphylla*, and *A. umbrinella*, which are also found in *A. rosea*, provide evidence, independent of morphology, that these species are among the sexual progenitors of the *A. rosea* complex.

Few comprehensive studies have been conducted on isozyme variation on clonal plant species (Ellstrand and Roose 1987); consequently it is difficult to compare *A. rosea* to other asexual plants. Values of A (average = 1.39 ± 0.129; table 2) are within the range of values found by Hamrick et al. (1979) and are significantly higher ($p = 0.0001$) than those A values for 33 populations of amphimictic species of *Antennaria* [1.28 (Bayer and Crawford 1986); 1.29 ± 0.163 (Bayer 1988)]. The average value of P (average = 0.29 ± 0.064; table 2) is similar to other perennial dicots (Hamrick et al. 1979) and significantly higher ($p = 0.0001$) than sexual species of *Antennaria* [0.22 (Bayer and Crawford 1986); 0.19 ± 0.103 (Bayer 1988)]. Observed H values (average = 0.229 ± 0.064; table 2) are equal to or, in many cases, higher than those reported for other plant groups (Hamrick et al. 1979). Compared to H_{obs} for amphimictic species of *Antennaria* [0.068 (Bayer and Crawford 1986); 0.065 ± 0.04 (Bayer 1988)], the values are significantly higher ($p < 0.0001$), and for other agamospermous species, i.e., *A. neodioica* Greene (0.137; Bayer and Crawford 1986), the values are also higher.

Gene diversity statistics (table 3) indicate that *Acp-1*, *Lap-1*, and *Pgi-3* contain the highest total diversity of those loci that were surveyed in *A. rosea*. H_T for all loci is 0.183, which is significantly higher ($p < 0.005$) than values found for nine amphimictic species of *Antennaria* (range = 0.062 to 1.36; Bayer 1988; Bayer and Crawford 1986). Values of P and A directly influence the magnitude of H_T; consequently it is not surprising to find that the value of H_T is higher for *A. rosea* than the sexual species of *Antennaria*, because the values for A and P are higher. Values of H_S (0.114; table 3), D_{ST} (0.069; table 3), and G_{ST} (0.378; table 3) are all higher than values for nine species of amphimictic *Antennaria*, in which the ranges of gene diversity statistics are H_S (0.037–0.087), D_{ST} (0.007–0.058), and G_{ST} (0.044–0.225) (Bayer 1988; Bayer and Crawford 1986). A comparison of values of H_S and D_{ST} indicates that the total diversity (H_T) is partitioned more within populations than between populations, in fact 37.8% (G_{ST}; table 3) of the variation is the result of interpopulational differences.

Average values of D (average $D = 0.058$; range

TABLE 2. Genetic variation in 33 populations of *Antennaria rosea*. 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); and observed average heterozygosity (H_{obs}). Population designations are given in table 1.

Population designations	A	P	H_{obs}
R1	1.40 ± 0.737	0.27	0.151
R2	1.27 ± 0.458	0.33	0.267
R3	1.50 ± 0.816	0.31	0.278
R4	1.31 ± 0.602	0.25	0.260
R5	1.56 ± 0.814	0.38	0.220
R6	1.64 ± 1.008	0.36	0.260
R7	1.27 ± 0.458	0.27	0.286
R8	1.14 ± 0.363	0.14	0.143
R9	1.27 ± 0.458	0.27	0.208
R10	1.47 ± 0.833	0.27	0.157
R11	1.24 ± 0.437	0.24	0.189
R12	1.50 ± 0.650	0.43	0.285
R13	1.33 ± 0.617	0.27	0.200
R14	1.38 ± 0.719	0.25	0.227
R15	1.53 ± 0.915	0.33	0.190
R16	1.44 ± 0.727	0.31	0.180
R17	1.54 ± 0.877	0.31	0.291
R18	1.31 ± 0.602	0.25	0.221
R19	1.44 ± 0.727	0.31	0.296
R20	1.42 ± 0.669	0.33	0.333
R21	1.35 ± 0.497	0.36	0.400
R22	1.40 ± 0.737	0.27	0.276
R23	1.33 ± 0.617	0.27	0.267
R24	1.27 ± 0.594	0.20	0.200
R25	1.60 ± 1.056	0.27	0.166
R26	1.08 ± 0.277	0.08	0.077
R27	1.27 ± 0.458	0.27	0.246
R28	1.33 ± 0.617	0.27	0.234
R29	1.50 ± 0.905	0.33	0.233
R30	1.54 ± 0.967	0.31	0.147
R31	1.40 ± 0.737	0.27	0.238
R32	1.31 ± 0.479	0.31	0.287
R33	1.44 ± 0.727	0.31	0.160
Averages (±s.d.)	1.39 ± 0.129	0.29 (±0.064)	0.229 (±0.064)

= 0.003–0.220) and I (average I = 0.944; range = 0.802–0.997) for all pairwise comparisons of 33 populations of *A. rosea* indicate that the populations within the species have diverged only slightly, as would be expected for intraspecific comparisons. The cluster analysis (UPGMA) of the D matrix of 33 *A. rosea* populations and eight populations representing taxa that are related to *A. rosea* (fig. 2) effectively portrays the relationship of the populations and species. Most of the *A. rosea* populations are most similar to

TABLE 3. Nei's genetic diversity statistics for 33 populations of *Antennaria rosea*. 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	H_T	H_S	D_{ST}	G_{ST}
Acp-1	0.590	0.434	0.156	0.264
Gdh-1	0.439	0.095	0.344	0.783
Lap-1	0.657	0.453	0.204	0.310
Lap-2	0.241	0.012	0.229	0.951
Pgi-3	0.523	0.421	0.102	0.195
Pgm-1	0.215	0.130	0.085	0.395
Skdh-1	0.381	0.267	0.114	0.300
Tpi-3	0.425	0.345	0.080	0.189
All loci	0.183	0.114	0.069	0.378

populations of *A. corymbosa*, *A. media*, *A. microphylla*, and *A. umbrinella*, whereas fewer populations are similar to *A. aromatica*, *A. densifolia*, *A. marginata*, and *A. rosulata*. Morphological studies have demonstrated that many *A. rosea* segregates resemble one particular sexual progenitor (Bayer, in press a) and this pattern is seen in several of the populations used in this study. For example, populations 3 and 31 morphologically resemble diploid *A. microphylla* and populations 5, 21, and 14 resemble diploid *A. corymbosa* and based on D they cluster closest to these diploids, respectively (fig. 2). Most *A. rosea* segregates do not morphologically resemble any one particular sexual species and represent polyploids of multiple hybrid origin from among several sexual species. Major geographic patterns of population relationships are not evident from the phenogram (fig. 2); however, in many cases, populations from the same region do have high I (low D) values and are consequently closely clustered.

Values of D and I for interspecific comparisons between *A. rosea* and its sexual relatives are presented in table 4, isozyme data for sexual species having been obtained from the results of previous studies (Bayer 1988; Bayer, in press b). Relationships among the sexual species have been discussed (Bayer 1988; Bayer, in press b), so only comparisons between *A. rosea* and the other species will be discussed in detail. Values of I between *A. rosea* and its relatives range from

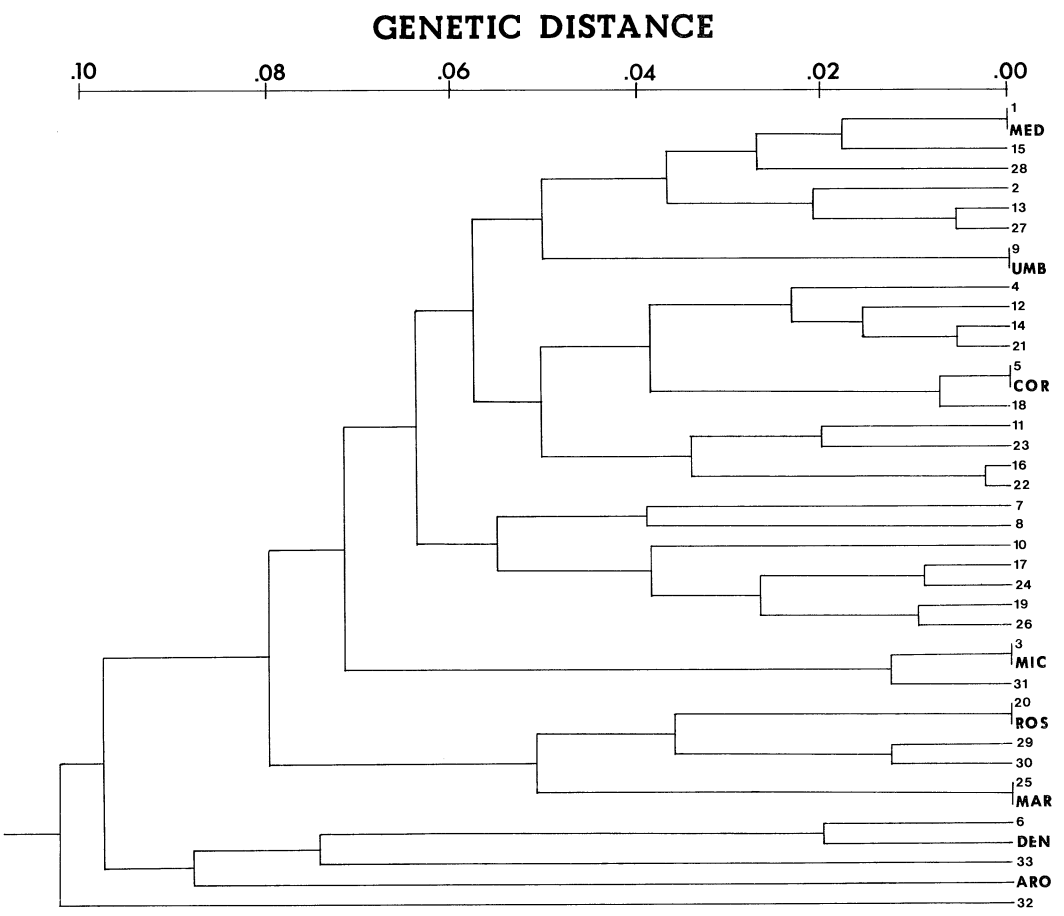

FIG. 2. Distance phenogram (UPGMA) derived from Nei's genetic distances of all pairwise comparisons of 33 populations of *Antennaria rosea* with eight sexual species of *Antennaria* (table 4), including *A. aromatica* (ARO), *A. corymbosa* (COR), *A. densifolia* (DEN), *A. marginata* (MAR), *A. media* (MED), *A. microphylla* (MIC), *A. rosulata* (ROS), and *A. umbrinella* (UMB). Population designations for the *A. rosea* populations are the same as those cited in table 1. Cophenetic correlation coefficient is 0.7946.

0.855 to 0.983 (table 4). The *I* values (table 4) indicate that *A. rosea* is most similar to *A. aromatica, A. corymbosa, A. media,* and *A. umbrinella,* then next most similar to *A. marginata* and *A. rosulata,* and least similar to *A. microphylla* and *A. densifolia.* Morphology indicates that *A. rosea* is most similar to *A. aromatica, A. corymbosa, A. media, A. microphylla,* and *A. umbrinella* (Bayer 1988).

DISCUSSION

It is interesting to compare the levels of genetic variation among sexual species and *A. rosea,* especially when the extremes in breeding systems between the two groups are considered. The sexual species are dioecious and consequently are obligate outcrossers, whereas *A. rosea* is an obligate gametophytic apomict and should have a population structure similar to that found in autogamous species. Loveless and Hamrick (1984) predicted that populations of obligate apomicts should have reduced amounts of genetic variation within and among populations when compared to populations of sexual species. However, values of A, P, H_{obs}, H_T, H_S, D_{ST}, and G_{ST} are significantly higher in populations of *A. rosea* than in sexual populations of *Antennaria.* This could be the result, in part, of their hybrid origin from among several amphimicts. Also, populations tend to be composed of one or a few, highly heterozygous ge-

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

Taxa	ARO	COR	DEN	MAR	MED	MIC	ROS	ROZ	UMB
A. aromatica (ARO)	*****	0.934	0.857	0.925	0.943	0.887	0.978	0.901	0.979
A. corymbosa (COR)	0.068	*****	0.891	0.908	0.990	0.842	0.944	0.894	0.950
A. densifolia (DEN)	0.155	0.116	*****	0.844	0.887	0.718	0.855	0.800	0.868
A. marginata (MAR)	0.078	0.097	0.170	*****	0.914	0.821	0.931	0.978	0.957
A. media (MED)	0.059	0.010	0.120	0.090	*****	0.848	0.938	0.897	0.954
A. microphylla (MIC)	0.119	0.172	0.332	0.198	0.165	*****	0.928	0.809	0.848
A. rosea (ROS)	0.022	0.057	0.157	0.071	0.064	0.075	*****	0.907	0.983
A. rosulata (ROZ)	0.105	0.112	0.223	0.023	0.109	0.213	0.098	*****	0.930
A. umbrinella (UMB)	0.021	0.051	0.141	0.044	0.047	0.116	0.017	0.073	*****

notypes yielding higher values of H_{obs}. The gene diversity statistics (H_T, H_S, D_{ST}, G_{ST}) indicate that *A. rosea* shows more interpopulational and intrapopulational gene diversity than the sexually reproducing species related to *A. rosea*. This is probably to be expected because agamospermy precludes genetic recombination and as a consequence increases intrapopulational substructuring and extends interpopulational divergence. Ellstrand and Roose (1987) have emphasized the fact that populations of apomicts are often composed of relatively large numbers of genotypes, contrary to previous beliefs that such populations were relatively depauperate with respect to clonal diversity. This seems to be true in *Antennaria* where populations generally are composed of many multilocus genotypes.

The origin of *A. rosea* is confounded as a consequence of the overwhelming morphological complexity of the group. Morphological characters that are unique to each of the sexual progenitor species can be detected in various combinations in the *A. rosea* segregates (Bayer, in press a). Based on morphology, the *A. rosea* polyploid agamic complex is a typical compilospecies, i.e., it is the result of hybridization from among several sexually reproducing diploids and tetraploids. The sexual species themselves, *A. aromatica, A. corymbosa, A. densifolia, A. marginata, A. media, A. microphylla, A. rosulata,* and *A. umbrinella,* have not diverged from each other to the extent that unique alleles occur at the loci surveyed (Bayer 1988; Bayer, in press b). Morphological differences among the sexual species may be due to relatively few genes, as has been suggested for other groups by Gottlieb (1984) in his review of the genetics of morphological differences. The sexual species of *Antennaria* follow a pattern that is similar to that found in other genera such as *Quercus* (Manos and Fairbrothers 1987), and *Heuchera* (Soltis 1985), in which relatively large amounts of morphological divergence have occurred among the species, but only moderate amounts of divergence at the enzyme loci.

The segregates of *A. rosea* should contain alleles that have their origins in the sexual taxa; however only *A. corymbosa, A. microphylla,* and *A. umbrinella* have alleles that are unique. Consequently, isozyme data can only be used as independent evidence to support the hypothesis that *A. corymbosa, A. microphylla,* and *A. umbrinella* are among the sexual progenitors of *A. rosea.* Values of *I* indicate that although the remaining species, *A. aromatica, A. densifolia, A. marginata, A. media* and *A. rosulata,* are genetically very similar to *A. rosea* segregates, they can be neither included nor excluded as ancestors of *A. rosea* based solely on isozyme data. Similar results were obtained for the *A. parlinii* Fernald and *A. neodioica* complexes (Bayer and Crawford 1986), where unique alleles of a few sexual progenitors could be used as separate evidence to document the genomic composition of those polyploids.

Antennaria rosea probably arose in the unglaciated southern Rocky Mountains because this is the region where the species is still sympatric with its diploid progenitors. *Antennaria rosea* is probably of recent origin as are its sexual progenitors. This is supported by the fact that the only novel allele found in *A. rosea,* not yet detected in the probable sexual progenitors, is *Pgm-1*^{a}. If the polyploids were relatively old, it would be likely that sufficient time would have elapsed such that more unique alleles would be found in the *A. rosea* complex. Similar results have

been found in other relatively youthful polyploids, such as *Tragopogon* (Roose and Gottlieb 1976).

Soltis and Rieseberg (1986) have stressed the need to evaluate various types of data from morphology, secondary product chemistry, cytogenetics, and enzyme electrophoresis before determining the type of polyploid speciation that has occurred. Morphology suggests that some of the segregates of *A. rosea* are autopolyploids because they closely resemble their sexual diploid relatives, whereas other segregates appear morphologically to be hybrid polyploids (allopolyploids) from among several diploids. Because the sexual parents are so similar genetically, one would expect that, although many of the polyploid offspring are of alloploid origin, isozymically the offspring would behave as autopolyploids and display multisomic inheritance, not the fixed heterozygosity characteristic of allopolyploids. Cytogenetic analysis to determine the mode of inheritance is not possible because staminate plants are absent from *A. rosea*. The isozyme data suggest a tetrasomic mode of inheritance, which is characteristic of autopolyploids (Soltis and Rieseberg 1986); however, fixed heterozygosity cannot be discounted. Consequently, it seems best to consider the *A. rosea* polyploids as occurring on the polyploid continuum from strict autopolyploids to segmental allopolyploids.

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