Investigations into the evolutionary history of the *Antennaria rosea* (*Asteraceae: Inuleae*) polyploid complex*

RANDALL J. BAYER

Abstract: The *Antennaria rosea* polyploid agamic complex is one of the most morphologically diverse and widespread complexes of N. American *Antennaria.* The group is taxonomically confusing because of numerous agamospermous microspecies, having been recognized as distinct species. Morphometric analyses have demonstrated that the primary source of morphological variability in the complex derives from six sexually reproducing progenitors, *A. aromatica, A. corymbosa, A. media, A. microphylla, A. racemona,* and *A. umbrinella.* Additionally, two other sexually reproducing species, *A. marginata* and *A. rosulata,* may have contributed to the genetic complexity of the *A. rosea* complex. Cluster analysis indicates that four discrete morphological groups exist within the *A. rosea* complex. Each group could be the result of predominance of genes from different groups of sexual progenitors. As *A. rosea* is of multiple hybrid origin, from among several sexual progenitors, it is advisable to recognize *A. rosea* as a distinct species from its sexual progenitors.

Antennaria rosea E. GREENE is one of the largest of the polyploid agamic complexes in *Antennaria* GAERTNER. *Antennaria rosea* is widespread in the western cordillera of N. America from southern California, Arizona and New Mexico north to the arctic from Alaska east to the shores of Hudson and James Bay. Additionally, *A. rosea* occurs disjunctly in the Canadian maritime provinces, eastern Quebec, and immediately north of and adjacent to Lake Superior. *Antennaria rosea* is found in a wide range of habitats from dry, sagebrush steppe, montane forests, and moist or dry alpine and arctic tundra.

ELIAS NELSON (1901) was probably the first to note that *A. rosea* is among the most morphologically polymorphic of all the western N. American *Antennaria.* *Antennaria rosea* has been treated variously, but most often recognized, in the strict sense to refer to clones with rose-colored phyllaries as described originally by E.

L. GREENE (1898). However, phyllary color is often a poor indicator of species delimitation in *Antennaria,* especially in *A. rosea.* Within populations of *A. rosea* phyllary color is usually quite variable, ranging from different combinations and shades of white, pink, green, red and brown (see herbarium collections at ALTA representing population diversity, BAYER & LEBEDYK M-507, UT-615, BAYER & STEBBINS I-304, BAYER & al. CO-459, CO-460, ID-603, UT-618, WY-505). In fact most of the different phyllary color morphs have been described as distinct species. The *A. rosea* complex is composed of a large number of individual agamospermous clones, or microspecies and because some of the populations of *A. rosea* are composed of single genotypes, and many of the microspecies have wide geographic ranges, they have often been recognized as distinct species (BAYER 1987a). Conversely, some populations are composed of many morphologically distinct microspecies.

Individuals of *A. rosea* reproduce by gametophytic apomixis and the species is almost always composed entirely of pistillate plants (BAYER 1987a, BAYER & STEBBINS 1983). Staminate plants are extremely rare, and when these are investigated they are found to possess inviable pollen grains (BAYER 1987a, and unpubl.). Sterile staminate clones of primarily agamospermous species have been termed "aberrant males" (STEBBINS 1932) to distinguish them from "normal" fertile staminate plants typical of amphimictic species. Clones of *A. rosea* are typically triploid ($2n = 42$) or tetraploid ($2n = 56$), only rarely pentaploid (BAYER 1984; BAYER & STEBBINS 1981, 1987).

The source of the variation within polyploid agamic complexes is the sexually reproducing species of the genus (BAYER 1985a, b, 1987a; GUSTAFSSON 1947; RICHARDS 1973). The first two investigations in this series (BAYER 1985a, b) showed that two other agamic complexes in *Antennaria, A. parlinii* FERN. and *A. neodioica* E. GREENE, were of multiple hybrid origin from among several extant sexual diploid/tetraploid species of *Antennaria.* This was subsequently supported by data from an isozyme electrophoretic study (BAYER & CRAWFORD 1986). Morphological characters typical of, or unique to, a particular sexual species can often be detected in the polyploid clones (BAYER 1985a, b). Most often clones display hybrid combinations of the morphological characters of several sexual progenitors (BAYER 1985a, b, 1987a). If several sexual species were the progenitors of the agamic complex, then an enormous number of hybrid combinations are possible and subsequent taxonomic confusion is inevitable (BAYER 1987a). BAYER (1987a, b) proposed that the *A. rosea* complex is the result of multiple hybridizations from among several amphimictic species of western N. America, namely *A. aromatica* EVERT, *A. corymbosa* E. NELSON, *A. marginata* E. GREENE, *A. media* E. GREENE (including *A. pulchella* E. GREENE), *A. microphylla* RYDB., *A. racemosa* HOOK., *A. rosulata* RYDB., and *A. umbrinella* RYDB. (Table 1).

The purpose of the present paper is to investigate the morphological variation within the *A. rosea* complex and to explore its relationship to the sexually reproducing species. Delimitation of the morphological variation within the *A. rosea* complex will provide a basis for the formal taxonomic revision of the complex currently underway.

Materials and methods

Specimens from ALTA, CAN, CAS, DAO, DAV, GH, ID, MONT, MONTU, NDG, NY, RM, UC, and US were used in the following multivariate analysis. A list of 42 characters

Table 1. Salient morphological features of sexual *Antennaria* spp. that occur in their allopolyploid derivatives. Presented are suites of characters that are characteristic to each of the sexual species followed by citation of specimens of polyploid *A. rosea* that possess some these characters (i.e., tend morphologically toward these sexual species). Collectors abbreviations are as follows: *BS* R. J. BAYER & G. L. STEBBINS; *BDSS* BAYER, M., DUN-FORD, R. SORENG, and STEBBINS; *BL* BAYER & D. LEBEDYK; *BLJ* BAYER, LEBEDYK, and M. JONCAS. Specimens at ALTA with duplicates of most of BAYER & al. collections deposited at RM (some at CAN) and originals of collections other than those of BAYER & al. deposited at CAN

A. aromatica – subalpine/alpine, pulvinate growth form, cuneate leaves with strong odor of citronella, plant glandular throughout. *Antennaria rosea* tending toward *A. aromatica*: BDSS CO-458, BDSS CO-435, BDSS CO-441 (pro parte), BL CO-519, and BL MT-532, CALDER & KUKKONEN 27360, CALDER, SAVILE, and FERGUSON 13781, and TAYLOR & FERGUSON 2973.

A. corymbosa – subalpine (alpine), basal leaves relatively large, linear to oblanceolate, phyllaries with white tips and distinctive black spot and base. *Antennaria rosea* tending toward *A. corymbosa*: BDSS CO-421, BDSS CO-431, BDSS CO-454, BDSS CO-474, BL CO-510, BS I-304, BL M-507, BLJ MT-604, CALDER & SAVILE 11732, CALDER, SAVILE, and FERGUSON 14537 and CALDER, SAVILE, and FERGUSON 12439.

A. media – strictly alpine, phyllaries black or black based with dark green tips, spatulate leaves. *Antennaria rosea* tending toward *A. media*: BDSS CO-436, BDSS CO-448, BDSS CO-459 (pro parte), BDSS CO-460 (pro parte), BDSS CO-455, BDSS CO-467, BLJ WY-617 (pro parte), BL WY-505, CALDER & SAVILE 11639, and TAYLOR & FERGUSON 2149.

A. microphylla – lower montane/steppe, relatively tall flowering stalks, phyllaries green base with white tips (sometimes pink or red in phyllaries), basal rosette with canescent, spathulate leaves and numerous stolons, cauline leaves relatively numerous and linear. *Antennaria rosea* tending toward *A. microphylla*: BDSS CO-456, BLJ ID-602, BLJ MT-631, BS M-331, BS M-317, TAYLOR & FERGUSON 2564, and TAYLOR & FERGUSON 2431.

A. racemosa – montane/subalpine, basal leaves large, orbicular to ovoid, multi-nerved, and glabrous adaxially, purple stalked glands on caulis, open-racemose arrangement of heads. *Antennaria rosea* tending toward *A. racemosa*: BS M-334, CALDER, PARMELEE, and TAYLOR 19952, and CALDER, PARMELEE, and TAYLOR 19149.

A. umbrinella – steppe to subalpine, umber to light brown colored phyllaries, stolons strongly upsurgent at the tips and usually woody. *Antennaria rosea* tending toward *A. umbrinella*: BS M-332, BLJ UT-606, BLJ UT-611, and BLJ UT-610

(25 vegetative and 17 reproductive) used to construct the basic data matrix may be found in BAYER (1987 b) (Table 1). Location data (latitude and longitude) for each collection site were used to determine whether any of the characters displayed geographic patterns of variation. The basic data matrix may be obtained from the author.

Herbarium specimens having both staminate and pistillate individuals were selected from among the sexual species, since amphimictic populations usually have equal frequencies of staminate and pistillate individuals (BAYER & STEBBINS 1983). Specimens of all species were selected from throughout their range and from "typical" or representative specimens of the species as well as those that were perceived to represent the morphological extremes in each group.

Data matrix number one consisted of 150 OTUs (13 OTUs of *A. aromatica*, 15 OTUs of *A. corymbosa*, 15 OTUs of *A. marginata*, 15 OTUs of *A. media*, 15 OTUs of *A. microphylla*, 15 OTUs of *A. rosulata*, 15 OTUs of *A. umbrinella*, and 47 OTUs of *A. rosea* s.l.). Mean

values, were calculated for all characters for each individual species using the BMDP (DIXON 1981) univariate statistics program (BMDP 5 D) to produce an average value OTU or centroid. A second matrix consisted of eight centroids (one for each species) plus the 47 OTUs of *A. rosea* to generate a 55 OTU data matrix. Matrix number three consisted of 47 OTUs of *A. rosea*.

Methods of analysis were similar to those used in previous morphological studies of *Antennaria* (BAYER 1985 a, b, 1987 b). The NT-SYS program (ROHLF 1987, ROHLF & al. 1974) was used to perform the principal components analyses (PCA) and cluster analysis. The BMDP program (DIXON 1981) was used to calculate univariate statistics such as means and standard deviations of characters. The data were standardized by the STAND sub-routine of NT-SYS, whereby each character in the raw data matrix was transformed to have a mean of zero and a standard deviation of unity (SNEATH & SOKAL 1973). The distance and similarity matrices were produced by the SIMINT subroutine of NT-SYS. The coefficients of distance were calculated using the average taxonomic distance algorithm (SOKAL 1961). Pearson product-moment coefficients of similarity (SNEATH & SOKAL 1973) were produced by the SIMINT subroutine of NT-SYS. The PCA (SNEATH & SOKAL 1973) was performed by the FACTOR subroutine of NT-SYS. The PCAs extracted three factors each that were subsequently plotted by the Mac Spin program (D^2 Software, Austin, Texas), which allows rotation of the three axes until suitable views are obtained. A cluster analysis by the unweighted pair-group method using arithmetic averages (UPGMA; SNEATH & SOKAL 1973) was computed using the TAXON subroutine of NT-SYS. Bivariate correlation analyses, comparing latitude and longitude with morphological characters, were performed by the BMDP program (DIXON 1981) to determine if any of the characters were correlated to geography.

The PCA and cluster analyses were used to compare *A. rosea* to putative sexual pro-genitors, as well as to investigate whether any subspecific clusters are recognizable within the *A. rosea* complex itself. PCAs were performed on matrices 1 and 2, whereas a UPGMA cluster analysis was carried out on matrix 3. Matrix 3 was used for bivariate correlation analyses and univariate statistics were obtained for each species using subsets of matrix 1.

Pearson product-moment coefficients of similarity were obtained for all pairwise com-parisons of OTUs of matrix 2. Mean values for each of the sexual species and *A. rosea* were entered into the analysis as centroids. The use of centroids instead of individual OTUs for the sexual species makes the 3-dimensional graph (Fig. 2) less complicated, yet still portrays their phenetic relationships with the *A. rosea* complex. Each OTU of *A. rosea* was compared, by the use of coefficients of similarity (Table 2), to the centroids of the sexual species in an effort to distinguish, which sexual species was most similar to each individual *A. rosea*. The usefulness of mean similarity coefficients in determining the parentage of hybrids (*A. rosea* in this case) has been demonstrated in several other morphometric studies (BARBER 1982; BAYER 1985 a, b; JENSEN & ESHBAUGH 1976 a, b; WHIFFIN 1973). Compu-tations were carried out on the AMDAHL computer at the University of Alberta.

Results

Seven sexual species of *Antennaria, A. aromatica, A. corymbosa, A. marginata, A. media, A. microphylla, A. rosulata,* and *A. umbrinella*, were initially selected as putative ancestors to *A. rosea* because they are similar morphologically to various agamospermous segregates of the complex and are parapatric with *A. rosea* over most of their ranges (pers. obs.; BAYER & STEBBINS 1987). Morphometric analyses have shown the sexual species to be distinct morphologically (BAYER 1987 b).

The first three principal components in the PCA of the sexual species and *A. rosea* (Fig. 1) account for 63% of the variation and the first nine factors have eigenvalues greater than 1.000, indicating that the characters are not highly cor-
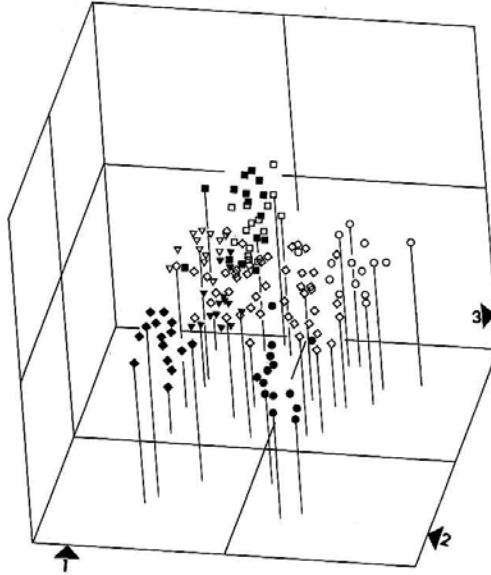
Fig. 1. PCA composed of 150 OTUs of ▽ *Antennaria aromatica,* ○ *A. corymbosa,* ▼ *A. marginata,* ■ *A. media,* ● *A. microphylla,* ◇ *A. rosea,* ◆ *A. rosulata,* and ☐ *A. umbrinella.* Factors 1 to 3 are labeled with arrowheads. This three-dimensional projection was obtained by rotation of PCA by the Mac-Spin program (D² Software, Austin, Texas)
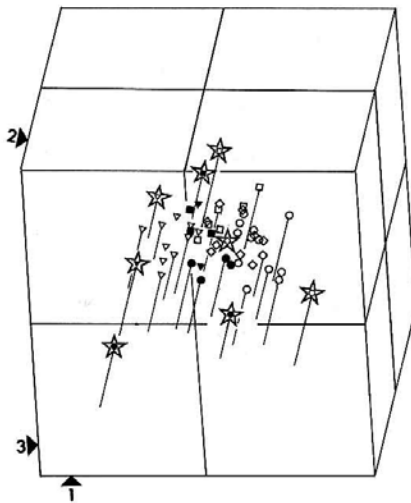

Fig. 2. PCA composed of 55 OTUs of *Antennaria.* The species composition of the OTUs is one centroid (stars with specific epithet symbols inside) each of ▽ *Antennaria aromatica,* ○ *A. corymbosa,* ▼ *A. marginata,* ■ *A. media,* ● *A. microphylla,* ◆ *A. rosulata,* and ☐ *A. umbrinella* and 47 OTUs of ◇ *A. rosea. Antennaria rosea* OTUs are labeled with the specific epithet symbol of the species to which it has the highest similarity as indicated by Pearson product-moment correlation coefficients (Table 2). This three-dimensional projection was obtained by rotation of PCA by the Mac-Spin program (D² Software, Austin, Texas)

related. High loadings for factor one include vegetative features such as length of basal leaves, stolon length, as well as reproductive characters like flowering stem height, length of the longest cauline leaf and heads per flowering stalk. Factor two has highest loadings for pistillate reproductive features primarily, such as pappus length, corolla length, and height of the involucre. Staminate phyllary width, sta-

Table 2. Table of Pearson product-moment coefficients of similarity between centroids of eight species of *Antennaria* and 47 OTUs of *A. rosea*. Highest similarity between each individual OTU and the centroids is indicated by an asterisk. Taxa are labeled with the first four letters of their specific epithets

| AROM	CORY	MARG	MEDI	MICR	ROSU	UMBR	ROSE
-0.518	0.517*	0.053	-0.288	-0.279	-0.287	-0.319	0.388
·0.380	-0.487·	-0.050	0.037	0.437*	0.300	0.141	-0.280
-0.019	-0.260	0.180	-0.424	0.332*	0.224	-0.488	-0.017
-0.184	0.367*	0.115	-0.541	0.279	-0.229	-0.258	0.095
-0.315	0.577*	-0.287	0.295	-0.241	-0.268	0.414	0.454
-0.250	0.235	-0.244	0.235	-0.182	-0.270	0.327	0.492*
-0.581	-0.030	-0.303	-0.089	-0.266	-0.263	-0.276	0.549*
-0.221	0.304*	-0.342	0.292	0.138	-0.003	0.276	0.164
-0.361	0.143	-0.241	-0.069	0.233	-0.273	0.046	0.402*
0.146	-0.138	0.221*	0.062	-0.346	0.033	-0.310	-0.239
-0.163	0.212	-0.328	0.268	0.140	-0.219	0.609*	0.433
-0.324	0.247	-0.252	-0.183	-0.008	-0.288	0.099	0.615*
-0.267	0.450*	-0.234	-0.177	0.256	-0.214	0.173	0.300
0.455	-0.303	-0.058	0.352	-0.230	0.183	0.526*	-0.113
-0.550	0.398	-0.222	-0.383	-0.056	-0.306	-0.313	0.653*
0.434	-0.187	-0.055	0.323	0.263	0.157	0.548*	-0.025
-0.060	0.483*	-0.127	-0.083	0.008	0.019	-0.195	0.029
-0.465	-0.025	-0.011	-0.151	-0.026	-0.155	-0.444	0.457*
-0.095	0.503*	-0.248	0.210	0.063	-0.198	0.440	0.301
0.116	-0.171	-0.263	0.407	0.150	-0.031	0.439*	0.124
-0.647	0.076	-0.316	-0.338	0.181	-0.276	-0.277	0.565*
-0.547	0.606*	-0.130	-0.326	-0.180	-0.274	-0.364	0.562
-0.424	0.594*	-0.110	-0.411	0.245	-0.142	-0.205	0.421
-0.353	0.288	-0.293	0.014	-0.045	-0.379	0.085	0.556*
-0.463	0.524	-0.189	-0.286	0.169	-0.306	-0.209	0.655*
-0.600	0.499	-0.201	-0.218	-0.227	-0.316	-0.309	0.553*
0.079	0.018	-0.121	0.493	-0.191	-0.087	0.547*	0.191
0.420*	-0.095	-0.120	0.259	-0.003	0.100	0.334	-0.035
-0.017	-0.046	-0.219	0.048	0.312*	-0.186	0.099	0.226
0.047	-0.268	-0.182	0.241*	-0.080	-0.025	0.236	0.094
-0.493	0.297*	0.179	-0.337	-0.243	-0.204	-0.467	0.217
-0.112	-0.036	0.112*	-0.134	-0.546	-0.115	-0.218	-0.071
-0.214	0.248*	0.069	-0.155	-0.531	·-0.256	-0.313	0.166
0.143	-0.039	-0.193	0.188	-0.106	-0.014	0.397*	-0.042
0.805*	-0.347	0.008	0.425	-0.019	0.327	0.376	-0.678
0.712*	-0.421	0.187	0.030	0.379	0.349	-0.088	-0.778
0.415*	-0.245	0.183	0.254	0.078	0.145	0.346	-0.522
0.444*	-0.346	-0.042	0.152	0.156	0.093	0.222	-0.438
0.564*	-0.374	0.221	0.243	-0.103	0.230	0.101	-0.558
0.335*	-0.274	0.050	0.190	-0.115	0.210	0.124	-0.374
-0.460	0.253	-0.079	-0.362	0.433*	-0.126	0.019	0.262
0.300*	-0.316	0.245	-0.183	-0.006	0.193	-0.293	-0.569
0.261	-0.338	-0.070	0.317*	-0.126	0.027	0.057	-0.330
-0.143	0.213*	0.133	-0.366	-0.066	0.120	-0.491	-0.195
0.500*	-0.502	0.147	0.211	-0.283	0.137	-0.061	-0.546
0.432	-0.502	0.215	0.636*	-0.062	0.221	-0.036	-0.751
0.456*	-0.416	0.308	-0.015	0.240	0.303	-0.291	-0.707
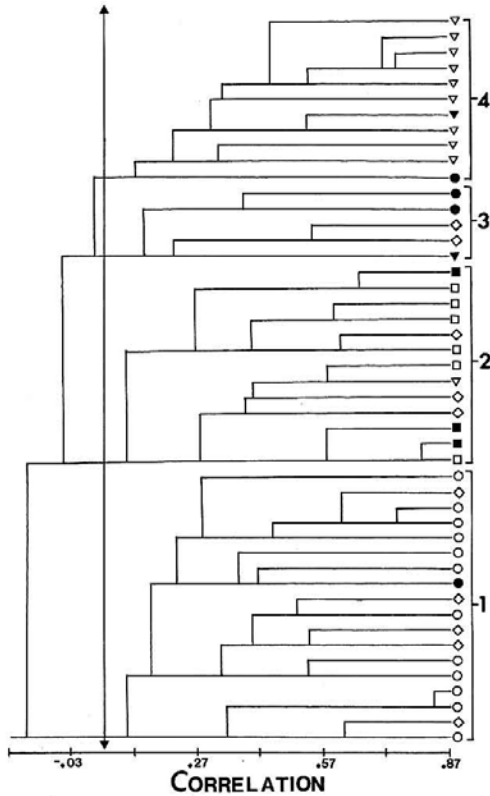
Fig. 3. Correlation phenogram (UPGMA) composed of 47 OTUs of *Antennaria rosea*. *Antennaria rosea* OTUs are labeled with the specific epithet symbol of the species to which it has the highest similarity as indicated by Pearson product-moment correlation coefficients (Table 2): ▽ *Antennaria aromatica*, ○ *A. corymbosa*, ▼ *A. marginata*, ■ *A. media*, ● *A. microphylla*, ◇ *A. rosea*, ◆ *A. rosulata*, and □ *A. umbrinella*. Cophenetic correlation coefficient is 0.838. Four phenons can be recognized at the level of similarity indicated by a phenon line (arrows)

minate head number per flowering stalk, and number of leaf nodes per flowering stalk have high loadings in factor three. The distinctness of the sexual species themselves (see BAYER 1987 b: 2391 − 2393, Figs. 1 − 5) is obscured by the addition of *A. rosea* to this analysis (Fig. 1). *Antennaria rosea* segregates occupy the center of the 3-dimensional space, whereas the sexual diploid/tetraploids form groups of OTUs surrounding the *A. rosea* OTUs. The apparent overlap between sexual *A. media* and *A. umbrinella* is an artifact of the angle of viewing because they actually separate best in the plane of factor one versus two. *Antennaria rosea* OTUs are morphologically intermediate between any of a number of the sexual species (Fig. 1).

Figure 2 portrays the PCA derived from matrix 2, in which the first three axes account for 70% of the variation and the first ten factors have individual eigenvalues greater than 1.000. Vegetative features such as stolon length, basal leaf length, as well as reproductive characters like pistillate flowering stem height, length of the longest cauline leaf on pistillate stems, heads per pistillate flowering stalk, and heads per staminate flowering stalk have high loadings in factor one. High loadings for factor two include not only reproductive features such as pistillate phyllary length, pistillate pappus length, and staminate corolla length, but the vegetative

feature of maximum width of the basal leaves. Factor three has highest loadings for reproductive features of the staminate plants such as involucre height, phyllary width, and corolla length. In most cases each *A. rosea* OTU had highest similarity, as indicated by Pearson product-moment correlation coefficients, with one of the sexual species, but in some cases OTUs of *A. rosea* had highest similarity with the *A. rosea* centroid and second highest with the centroid of a sexual species (Table 2). The species to which each *A. rosea* OTU is most similar, as determined by correlation coefficients (Table 2), is indicated by using species specific symbols for the 47 *A. rosea* OTUs (Fig. 2). The 47 *A. rosea* OTUs (Fig. 2) are surrounded by the seven centroids of the sexual species. *Antennaria rosulata* is remote to *A. rosea* and no *A. rosea* has highest similarity (Table 2) with the average OTU of *A. rosulata* (Fig. 2). The centroid of *A. rosea* is in a central position in the *A. rosea* cluster of OTUs (Fig. 2). Individual *A. rosea* OTUs are usually close phenetically to the sexual species to which they bear the highest morphological similarity as indicated by similarity coefficients (Table 2). A large number of *A. rosea* OTUs are most similar to one of two sexual species, *A. aromatica* or *A. corymbosa*, whereas only two OTUs (Fig. 2) are most similar to *A. marginata* (Table 2).

A cluster analysis was performed on the *A. rosea* complex to determine whether any intraspecific groups could be recognized within this polymorphic polyploid complex. The results of the cluster analysis (Fig. 3) suggest that four groups are detectable. Because each group has highest morphological similarity with one or two sexual species, it can be inferred that each group appears to be the product of gene combinations from different groups of the sexuals. This is supported by each individual OTU's morphological similarity to particular taxa using similarity coefficients (Table 2) and from personal observations of gross morphology of members of the groups (BAYER, pers. obs.). The first group contains specimens that are most similar to those GREENE (1898) cited in his original description of *A. rosea*, but these specimens also closely resemble larger-leaved diploids *A. corymbosa* and *A. racemosa*. The second has members that resemble the sexual species with dark-colored phyllaries, *A. media* and *A. umbrinella*. The species with light-colored phyllaries, *A. aromatica*, *A. marginata*, and *A. microphylla* appear to have closest affinities with the third and fourth groups. Group three is more similar to *A. microphylla* and *A. marginata*, whereas group four is almost exclusively represented by specimens resembling *A. aromatica*.

Very few characters in the *A. rosea* complex show any clinal variation with respect to latitude and longitude. The presence of stalked glands on the caulis and foliage is negatively correlated ($p \leqslant 0.05$) with longitude, whereas maximum width of the basal leaves, phyllary length, and length of the longest stolon leaf are positively correlated ($p \leqslant 0.05$) with latitude. The remaining characters show no significant correlation ($p > 0.05$) with latitude or longitude.

Discussion

Polyploid agamic complexes in *Antennaria* are well known for their perplexing morphological diversity (BAYER 1987 a). As a result of agamospermous seed production, a very large number of apomictic microspecies (agamospecies) can arise, each having the appearance of a distinct species. However, when all the microspecies

are considered as a group they blend into one another and the morphological discontinuities between the microspecies seem insignificant.

Previous studies (BAYER 1985 a, b, 1987 b) have demonstrated that diploid/autotetraploid sexual species of *Antennaria* are morphologically distinct from one another. Hybridization among the sexual taxa and subsequent polyploidization and acquisition of an agamospermous mode of reproduction by those hybrids yields the "crystallized" hybrids or agamospecies (BAYER 1987 a, RICHARDS 1973). Some of the agamic clones are almost indistinguishable morphologically from their progenitors, except that they are always pistillate, and this obscures the morphological distinctness of the sexual species themselves. Clearly, the only way to comprehend the morphological variation found in the agamic complex is to study the sexual progenitors of the complex. Once morphological variation in sexual species is delimited then that of the polyploids can be better understood and explained.

Previous morphometric studies have shown that other agamic complexes (BAYER 1985 a, b) are of multiple hybrid origin from among several sexual progenitors. The *A. parlinii* complex is related to the sexual diploids *A. plantaginifolia* (L.) RICHARDSON, *A. racemosa*, *A. solitaria* RYDB., whereas *A. neodioica* is related to *A. neglecta* E. GREENE, *A. plantaginifolia*, *A. racemosa*, and *A. virginica* STEBBINS. Morphological overlap among the polyploid complexes is the result of commonly shared diploid genomes, i.e., pivotal genomes (BAYER 1987 a).

Morphological variation (BAYER 1987 b) and biochemical divergence (BAYER 1988) of the putative sexual progenitor species of *A. rosea* have been assessed. It has been determined that *A. aromatica*, *A. corymbosa*, *A. marginata*, *A. media*, *A. microphylla*, *A. racemosa*, *A. rosulata*, and *A umbrinella* have diverged with respect to both morphology and genes encoding soluble enzymes (BAYER 1987 b, 1988, 1989). *Antennaria corymbosa*, *A. microphylla*, *A. racemosa*, and *A. rosulata* are strictly diploid (2 n = 28), whereas *A. aromatica*, *A. marginata*, *A. media*, and *A. umbrinella* have both diploid and tetraploid cytotypes (BAYER & STEBBINS 1987). The sexual tetraploid cytotypes are, in most cases, morphologically indistinguishable from the diploid cytotypes, except *A. media* in which diploids are noticeably smaller in many attributes (BAYER 1987 b, 1989). Each of the diploids has unique morphological characters and these appear in certain segregates of the *A. rosea* complex (BAYER, pers. obs.) (Table 1). It has been proposed that *Antennaria* has undergone rapid evolution in western N. America where morphological and habitat divergence has not been accompanied by an equivalent degree of isozyme divergence (BAYER 1987 a, 1988, 1989).

Antennaria rosea is the result of hybridization from among as many as eight sexual progenitors, however, two are probably of marginal importance in the genetic composition of the species (Fig. 4). The PCAs (Figs. 1 and 2) and similarity coefficients (Table 2) clearly indicate the hybrid nature of the *A. rosea* complex. It is phenetically intermediate to the diploids and many of the segregates of *A. rosea* bear close resemblance to several of the diploids (Figs. 1–4). Each of the diploids has characteristics that can be used as morphological markers (listed in Table 1) and these appear in different combinations in the hybrid gametophytic apomicts. For example, *A. corymbosa* has relatively large basal leaves that are linear to oblanceolate in outline, phyllaries that are white with a distinctive black spot or band at their base, and occurs in very mesic subalpine to alpine habitats along streams with *Salix* and/or *Potentilla fruticosa* (Table 1). Some segregates of *A.*
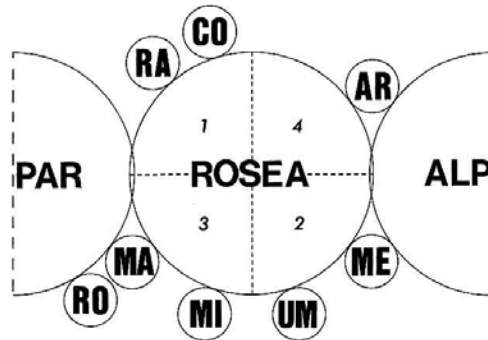
Fig. 4. Diagrammatic relationship of the *A. rosea* polyploid agamic complex to the *A. alpina* and *A. parvifolia* complexes and to it sexual progenitors. The size of each species group is a portrayal of the relative amounts of morphological variation within each taxon. Overlap of groups indicates slight morphological overlap between the agamic complexes. Sexual progenitors: AR *A. aromatica*, CO *A. corymbosa*, MA *A. marginata*, ME *A. media*, MI *A. microphylla*, RA *A. racemosa*, RO *A. rosulata*, and UM *A. umbrinella*. Polyploid complexes are labeled as follows: ALP *A. alpina*, PAR *A. parvifolia*, and ROSEA *A. rosea*. Some sexual species (AR, MA, and ME) are pivotal genomes because they have probably contributed genes to more than one complex. *Antennaria rosea* is divided into four groups, as was indicated by cluster analysis (Fig. 3), and similarity of each group to certain sexual species is indicated by the position of each sexual in relation to the groups. See text for further explanation

rosea that occur in similar habitats also display some of these distinctive morphological features, but instead of being sexually reproducing and diploid, as is *A. corymbosa*, they are agamospermous and triploid or tetraploid (BAYER & STEBBINS 1987) (Table 1). This analogy can also be extended to the other sexual species (Table 1).

The phenetic analyses (Figs. 1 – 3), as well as personal observations of field and herbarium materials, indicate that *A. aromatica*, *A. corymbosa*, *A. media*, *A. microphylla*, and *A. umbrinella* are the major sexual progenitors of the *A. rosea* complex (Fig. 4). Some white-phyllaried segregates of *A. rosea* bear a very close resemblance to *A. microphylla* and populations of these *A. rosea* clones can only be distinguished from *A. microphylla* in that they are more robust and are composed entirely of pistillate clones. Incidentally, the rose phyllary color in some *A. rosea* clones is not prevalent in any of the sexual taxa, but does occur sporadically in *A. marginata*, *A. microphylla,* and *A. umbrinella* and presumably was inherited from these sexual taxa by *A. rosea*. There is weak evidence indicating that *A. marginata* or *A. rosulata* may have contributed to the genetic composition of *A. rosea*, as very few clones of *A. rosea* display morphological characteristics that can be attributed to these species (Fig. 4). *Antennaria marginata* and *A. rosulata* are possibly the sexual progenitors of the *A. parvifolia* polyploid complex (BAYER 1987a) (Fig. 4).

Antennaria racemosa is a sexual diploid that is morphologically very different from the other sexual species (BAYER 1987b) (Table 1). Consequently, when included in PCA it caused all the OTUs of the other species to become clumped

together, therefore could not be included in the formal analysis (see BAYER 1987 b: 2391, Fig. 1). Evidence from observations in the field and herbarium indicate that some segregates of *A. rosea* have morphological features that indicate *A. racemosa* may have been a diploid progenitor. *Antennaria racemosa* has large, glabrous basal leaves, an open, racemose arrangement of heads, and purple stalked glands on its cauline leaves and peduncle (BAYER 1987 b) (Table 1). These characters are seen in *A. rosea* segregates that have often been identified as the microspecies *A. alborosea* A. E. PORSILD. This unique combination of characters is not found in any other amphimictic species of *Antennaria* so they must be attributed to parentage involving *A. racemosa*.

The four groups recognized by cluster analysis (Figs. 3 and 4), could be the result of predominance of genes from one or two sexual species in the genetic makeup of the individual groups. These groups should be recognized as subspecific categories of *A. rosea* (BAYER, unpubl.), because they are recognizable morphologically and they may each have had origins from different groups of sexual progenitors (Fig. 4). Consequently, these subspecific taxa would be established based upon evolutionary relationships of the groups, each having affinities with different sexual species.

The sexual species occur primarily in the southern half of the Rocky Mountain floristic region and the great basin province of the madrean floristic region (sensu CRONQUIST 1982) south of the Wisconsinan glacial maximum, except *A. microphylla* and *A. media*, which extend into the northern sections of the Rocky Mountain floristic region (see BAYER & STEBBINS 1987 for distribution maps of all the species). *Antennaria rosea* is much more widespread, having disjunct populations in the eastern half of the Canadian floristic province, north of Lake Superior (HYYPIO 1952), on the shore of James Bay (BOUCHARD & al. 1983), and in the Canadian maritime provinces [as *A. gaspensis* (FERN.) FERN., *A. straminea* FERN., and *A. subviscosa* FERN.]. Based on present day distributions of the species and glacial history of N. America, the most parsimonious model for the origin and migration of *A. rosea* is as follows. The sexual progenitors of *A. rosea* occur in mountains of the western United States and this is probably the region where *A. rosea* originated. During the Wisconsinan glacial period many cordilleran species migrated eastward (GIVEN & SOPER 1981, MARQUIS & VOSS 1981, WELLS 1970, WHITEHEAD 1972) including *A. rosea*. This is evidenced by disjunct populations of *A. rosea* on the shores of Lake Superior (HYYPIO 1952) and segregates of the complex (*A. gaspensis, A. straminea*, and *A. subviscosa*) that occur in the Gulf of St. Lawrence region, including the Gaspe peninsula, Anticosti Island and Newfoundland (FERNALD 1945, BOUCHARD & al. 1983). The habitat of the populations from Atlantic Canada [i.e., dry (calcareous) talus slopes and ledges, FERNALD 1924, 1933, 1945], is similar to that of many of western populations of *A. rosea* (especially those closely related to the sexual species *A. aromatica, A. media*, and *A. umbrinella*). Both morphological and habitat evidence support inclusion of these species in the *A. rosea* complex. Following the continental glacial retreat, *A. rosea* migrated north from the southern Rockies into the northern half of the Rocky Mountain floristic region and the western and central portions of the Canadian floristic province (sense CRONQUIST 1982). The sexual species, except *A. microphylla* and *A. media*, have small ranges in comparison to that of the *A. rosea* agamic complex (BAYER & STEBBINS 1987) and have not migrated into regions that were covered by con-

tinental glaciers during the Wisconsinan glacial period. Despite the relatively large number of morphological characters that display clinal variation in the sexual species (Bayer 1987 b), the *A. rosea* segregates show clinal variation for only a few morphological characters and this could possibly be the result of the relatively recent expansion of *A. rosea* into the glaciated region as opposed to the older and possibly more stable ranges of the sexual species. Ongoing investigations to obtain information regarding clonal genotype diversity in populations of *A. rosea* from the region of overlap with the sexual species in comparison with those from the northern margin of the range in the arctic and disjunct populations in the east, hopefully will provide further information in support of this model. It might be expected that clonal genotypic diversity within populations of *A. rosea* will decrease in the populations in the north and east, away from the center of diversity in the western United States. There is some evidence indicating that genotypic diversity decreases with increasing latitude in a number of plant and animal taxa (Fischer 1960, Hebert & Crease 1983, Weider & Hebert 1987).

One perplexing question regards the evolution of additional clones to the *A. rosea* complex (Bayer 1987 a). If *A. rosea* is entirely agamospermous, how then do new clones arise? Perhaps occasional sexual embryo sacs are produced by *A. rosea* clones and these are subsequently fertilized by sperm from compatible pollen donated by sexual relatives. This would explain the presence of large numbers of triploid *A. rosea* clones, as progeny between tetraploid *A. rosea* and a diploid sexual species. Most communities that contain *Antennaria*, include only one species of *Antennaria*, but several include a mixture of *A. rosea* with individuals of one sexual species (see the following examples at ALTA: *A. corymbosa* co-occurring with *A. rosea*, Bayer & Lebedyk CO-509 and CO-510, Bayer & al. UT-618 and UT-619; *A. microphylla* co-occurring with *A. rosea*, Bayer & al. WY-600 and WY-601, Bayer & al. MT-734 and MT-735, Bayer & al. MT-736 and MT-737; *A. media* co-occurring with *A. rosea*, Bayer & al. WY-616 and WY-617, Bayer & al. CA-700 and CA-701, Bayer & al. CA-707 and CA-708; *A. racemosa* co-occurring with *A. rosea*, Bayer & al. M-613 and M-614, Bayer & al. M-638 and M-639; *A. rosulata* co-occurring with *A. rosea*, Bayer & al. CO-702 and CO-703; *A. umbrinella* co-occurring with *A. rosea*, Bayer & al. ID-601 and ID-602, Bayer & al. M-630 and M-631). This would provide ample opportunity for the occurrence of introgression of genes from the sexual species into *A. rosea*.

To some degree, *Antennaria rosea* overlaps morphologically with the *A. alpina* (L.) Gaertner and *A. parvifolia* Nutt. polyploid agamic complexes (Bayer 1987 a) (Fig. 4). The reason being that most of the agamic complexes in *Antennaria* share one or two sexual genomes in their genetic composition (Bayer 1985 a, b, 1987 a; Bayer & Crawford 1986). *Antennaria rosea* probably shares genomes of *A. aromatica* and *A. media* with the *A. alpina* complex and *A. marginata* with the *A. parvifolia* complexes and consequently some agamospermous segregates are in the morphological "gray area" where the complexes overlap in morphology (Bayer 1987 a) (Fig. 4). Although *A. rosea* shares the diploid genome of *A. racemosa*, with the *A. neodioica* and *A. parlinii* complexes (Bayer 1985 a, b) the morphological overlap between *A. rosea* and the other two complexes is not as evident. The *A. rosea* complex can be described from a morphological/genetic/reproductive viewpoint as: Those primarily triploid and tetraploid, agamospermous, pistillate clones that contain genes from *A. aromatica*, *A. corymbosa*, *A. microphylla*, *A. media*, *A.*

racemosa, or *A. umbrinella*, and to lesser extent *A. marginata* and possibly *A. rosulata* (Fig. 4). The *A. rosea* complex should be considered to be in a mature stage of development (sensu GRANT 1981) because most, or all of the sexual progenitors, are still extant, and there are a large number of widely distributed agamospecies. From a taxonomic perspective, as has been reiterated before (BAYER 1987 a, BAYER & STEBBINS 1982), it seems best to recognize the *A. rosea* complex as a separate taxonomic and evolutionary entity apart from its sexually reproducing progenitors, because it is undoubtedly of multiple hybrid origin from among several amphimictic species. The indiscriminate lumping of sexual diploid and tetraploid lineages with hybrid polyploid agamospermous taxa, in my view (BAYER 1987 a), misrepresents the evolutionary relationships among the lineages.

References

BARBER, S. C., 1982: Taxonomic studies in the *Verbena stricta* complex (*Verbenaceae*). – Syst. Bot. **7**: 433–456.

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

– 1985 a: Investigations into the evolutionary history of the polyploid complexes in *Antennaria* (*Asteraceae: Inuleae*). 1. The *A. neodioica* complex. – Pl. Syst. Evol. **150**: 143–163.

– 1985 b: Investigations into the evolutionary history of the polyploid complexes in *Antennaria* (*Asteraceae: Inuleae*). 2. The *A. parlinii* complex. – Rhodora **87**: 321–339.

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

– 1987 b: Morphometric analysis of western North American *Antennaria* GAERTNER (*Asteraceae: Inuleae*). 1. 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*). 1. Sexual species of section *Dioicae*. – Syst. Bot. **13**: 525–537.

– 1989: Patterns of isozyme variation in western North American *Antennaria* (*Asteraceae: Inuleae*). 1. Diploid and polyploid species of section *Alpinae*. – Amer. J. Bot. **76**: 679–691.

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

– STEBBINS, G. L., 1981: Chromosome numbers of North American species of *Antennaria* GAERTNER (*Asteraceae: Inuleae*). – Amer. J. Bot. **68**: 1342–1349.

– – 1982: A revised classification of *Antennaria* (*Asteraceae: Inuleae*) of the eastern United States. – Syst. Bot. **7**: 300–313.

– – 1983: Distribution of sexual and apomictic populations of *Antennaria parlinii*. – Evolution **37**: 555–561.

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

BOUCHARD, A., BARABE, D., DUMAIS, M., HAY, S., 1983: The rare vascular plants of Quebec. — Nat. Mus. Can. Syllogeus **48**.

CRONQUIST, A., 1982: A map of the floristic provinces of North America. — Brittonia **34**: 144—145.

DIXON, N. J., 1981: BMDP statistical software. — Berkeley, CA: University of California Press.

FERNALD, M. L., 1924: The dwarf antennarias of northeastern America. — Rhodora **26**: 95—107.

— 1933: Recent discoveries in the Newfoundland flora. — Rhodora **35**: 327—343.

— 1945: Key to *Antennaria* of the "manual range". — Rhodora **47**: 221—239.

FISCHER, A. G., 1960: Latitudinal variation in organic diversity. — Evolution **14**: 64—81.

GIVEN, D. R., SOPER, J. H., 1981: The arctic-alpine element of the vascular flora of Lake Superior. — Natl. Mus. Nat. Sci. (Ottawa) Publ. Bot. No. **10**.

GRANT, V., 1981: Plant speciation. 2nd edn. — New York: Columbia University Press.

GREENE, E. L., 1898: Studies in the *Compositae*. — Pittonia **3**: 281.

GUSTAFSSON, Å., 1947: Apomixis in higher plants. — Acta Univ. Lund. Kungl. Fysiogr. Sallsk. Handl. N. R. Avd. 2, **42—44**: 1—370.

HEBERT, P. D. N., CREASE, T. J., 1983: Clonal diversity in populations of *Daphnia pulex* reproducing by obligate parthenogenesis. — Heredity **51**: 353—369.

HYYPIO, P. A., 1952: *Antennaria rosea* GREENE in the Lake Superior region. — Rhodora **54**: 291.

JENSEN, R. J., ESHBAUGH, W. H., 1976a: Numerical taxonomic studies of hybridization in *Quercus*. 1. Populations of restricted areal distribution and low taxonomic diversity. — Syst. Bot. **1**: 1—9.

— — 1976b: Numerical taxonomic studies of hybridization in *Quercus* 2. Populations with wide areal distributions and high taxonomic diversity. — Syst. Bot. **1**: 10—19.

MARQUIS, R. J., VOSS, E. G., 1981: Distributions of some western North American plants disjunct in the Great Lakes region. — Michigan Bot. **20**: 53—82.

NELSON, E., 1901: A revision of certain species of plants of the genus *Antennaria*. — Proc. U.S. Nat. Mus. **23**: 697—713.

RICHARDS, A. J., 1973: The origin of *Taraxacum* microspecies. — Bot. J. Linn. Soc. **66**: 189—211.

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

— KISHPAUGH, J., KIRK, D., 1974: Numerical taxonomy system and multivariate statistical programs. — Stony Brook, NY: State University of New York.

SNEATH, P. H. A., SOKAL, R. R., 1973: Numerical taxonomy. — San Francisco: Freeman.

SOKAL, R. R., 1961: Distance as a measure of taxonomic similarity. — Syst. Zool. **10**: 70—79.

STEBBINS, G. L., 1932: Cytology of *Antennaria*. 1. Normal species. — Bot. Gaz. (Crawfordsville) **94**: 134—151.

WEIDER, L. J., HEBERT, P. D. N., 1987: Ecological and physiological differentiation among low-arctic clones of *Daphnia pulex*. — Ecology **68**: 188—198.

WELLS, P. V., 1970: Postglacial vegetational history of the Great Plains. — Science **167**: 1574—1582.

WHIFFIN, T., 1973: Analysis of a hybrid swarm between *Heterocentron elegans* and *H. glandulosum* (*Melostomataceae*). — Taxon **22**: 413—423.

WHITEHEAD, D. R., 1972: Approaches to disjunct populations: the contribution of palynology. — Ann. Missouri Bot. Gard. **59**: 125—137.

Address of the author: RANDALL J. BAYER, Department of Botany, University of Alberta, Edmonton, Alberta T6G 2E9, Canada.