Antennaria rosea (Asteraceae) - A model group for the study of the evolution of polyploid agamic complexes

Randall J. Bayer

Antennaria (Asteraceae: Gnaphalieae) is useful as a tool for studying polyploid agamic complexes because both polyploidy and agamospermy are widespread in this genus. They are dioecious, perennial herbs that occur throughout temperate and arctic regions of the northern hemisphere, with the major center of diversity in the Rocky Mountains of North America. The diploids are morphologically well-defined and usually have rather restricted geographic ranges. The five polyploid complexes in the genus differ considerably from one another with respect to ploidy levels, morphological variation and reproductive modes. The triploid/tetraploid gametophytic apomict, *A. rosea*, is one of the most thoroughly examined complexes in the genus and it is used to illustrate the evolution of a typical *Antennaria* polyploid agamic complex The *A. rosea* polyploid complex has a wider geographic range and possibly greater ecological amplitude than its diploid progenitors and is the result of multiple hybrid origin from among as many as eight sexual diploid species. The diploids gave rise to *A. rosea* through the processes of interspecific hybridization and backcrossing among themselves and probably through hybridization with facultatively sexual apomicts. The agamic complexes, including *A. rosea*, may be morphologically confluent with one another because they share sexual progenitors.

R. J. Bayer, University of Alberta, Department of Biological Sciences, Edmonton, Alberta, T6G 2E9, Canada. Present address: CSIRO - Division of Plant Industry, Centre for Plant Biodiversity Research, GPO Box 1600, Canberra, ACT, 2601, Australia

Introduction

Investigations into the evolution of polyploid agamic complexes represent considerable challenges to evolutionary botanists. Groups such as *Antennaria*, *Bouteloua*, *Crataegus*, *Crepis*, *Hieracium*, *Poa*, *Potentilla*, *Rubus*, *Taraxacum* and *Townsendia* are well known for their taxonomic complexity and as a result they have been somewhat ignored by most modern biosystematists. *Antennaria* Gaertner (Asteraceae: Gnaphalieae) is a genus which has several interesting evolutionary and morphological features such as gametophytic apomixis,

polyploidy, and sexual dioecism, making it a suitable tool to use when studying the evolution of polyploid agamic complexes. [Throughout the text "apomixis" means seed apomixis, or agamospermy. Therefore, as used here, "apomicts" are agamospermous microspecies.]. About 350 species of *Antennaria* have been described world-wide, but most of these are apomictic microspecies because in the past taxonomic practice has been to give each species status (Bayer & Stebbins 1993).This has led to unwieldy taxonomic classifications, which only a few experts on each group can use (Bayer & Stebbins 1993). Additionally, these types of

classifications reveal little about the evolutionary relationships or phylogenies of the agamic complexes.The only way to study the evolution of agamic complexes is through an integrated series of investigations including morphology, cytogenetics, phytogeography, ecology, enzyme electrophoresis, DNA sequence data, and RAPDs (random amplified polymorphic DNA). This example from *Antennaria* demonstrates how some of these data can be integrated to reveal clues to the phylogenetic origin of the polyploid agamic complex.

Evolution of the typical polyploid agamic complex

Agamic complexes typically include a series of polyploid sexual, facultatively or obigately agamospermous microspecies, which are largely the result of various hybridizations among sexual diploid and sexual polyploid members of the complex. If several diploids have contributed genes to the complex, then a considerable number of microspecies evolve because each microspecies can be of different multiple hybrid origin. The sexual diploid (and sometimes sexual autotetraploid) relatives are distinct morphologically from one another, but have a much greater amount of morphological variation than any single microspecies. The initial steps in the formation of the agamic complex involve hybridization among the sexual diploids which give rise to polyploids at many different ploidy levels. Generally, the polyploids at the lower levels (triploids and tetraploids) reproduce sexually and consequently there is a possibility for gene exchange among them. At higher ploidy levels, where agamospermy is primarily obligate, the microspecies are reproductively isolated from one another. The morphological variation among various obligately agamospermous microspecies is slightly discontinuous because of their reproductive isolation. Some clones tend to merge morphologically into their sexual relatives, especially if they have a significant number of genes from a single sexual taxon. Consequently, this obscures the morphological distinctness of the sexual diploids themselves. Perhaps genes from the sexual diploids can continue to be relocated, via introgressive gene flow, into the agamic complex through sexual triploid and tetraploid members of the complex. Unbalanced cytotypes such as triploids, pentaploids, septaploids, and various aneuploids can reproduce easily via agamospermy and therefore any hybrid has the potential to become fertile. The resultant polyploid agamic complex is comprised of a myriad clones that appear morphologically to represent a giant hybrid swarm, which is usually of multiple hybrid origin from among several sexual relatives.

The genus Antennaria

Antennaria is a moderate-sized genus of about 40 recognized species and belongs to the tribe Gnaphalieae of the Asteraceae (Bayer, Soltis, & Soltis, in press). It is a peculiar member of the Gnaphalieae not only because of the predominance of features such as agamospermy, polyploidy and sexual dioecism, but also in its distribution. Most Gnaphalieae occur in southern Africa and Australia (see Anderberg 1989, 1991, for a systematic monographs of the Gnaphalieae), whereas *Antennaria* is confined largely to the northern hemisphere, especially North America, with several unstudied taxa from the Andes of South America (Cabrera 1957).

Antennaria are dioecious, herbaceous, usually stoloniferous, perennials with simple, entire basal leaves and ± reduced cauline leaves. The flowering stalks are composed of one to many capitula and the pistillate and staminate capitula and florets are sexually dimorphic. The white or more often colored involucral bracts, imbricated in several series, are dry and scarious. The base chromosome number in *Antennaria* is $x = 14$ and taxa with $2n = 28$ have been considered to be diploids by North American authors (Stebbins 1932a; Bayer & Stebbins 1981; Bayer 1984; Bayer & Stebbins 1987). The genus consists of 33 known sexual diploid/tetraploid species and at least five large polymorphic polyploid agamic complexes (Bayer 1990a).

A morphology-based cladistic analysis of 32 sexual diploid species (Bayer 1990a) provided the first phylogenetic hypothesis for the sexually reproducing species, revealing that the genus comprises five constitutive monophyletic groups, Geyeriae, Argenteae, Dimorphae, Pulcherrimae (= Carpaticae sensu Urbanska; Urbanska (1983a, 1983b)), and Catipes. This cladistic analysis (Bayer 1990a) did not delineate *Antennaria* as a monophyletic group, but found that *Antennaria* would be monophyletic only if *A. geyeri* (Geyeriae) was withdrawn from the genus. Additionally, cpDNA restriction site data (unpublished data) indicated that *Antennaria* was monophyletic only with the inclusion of *Anaphalis* within *Antennaria*. Because the earlier cladistic analysis based on morphology (Bayer 1990a) did not fully resolve the phylogeny of *Antennaria* a different technique utilizing molecular data was investigated.

The internal transcribed spacer regions (ITS-1 & ITS-2) of nuclear ribosomal DNA were sequenced for 30 sexual diploid species of *Antennaria* and one species from each of the outgroup genera *Anaphalis*, *Ewartia*, *Leontopodium*, and *Pseudognaphalium* (Bayer, Soltis, & Soltis, in press). ITS sequences have been very useful in reconstructing the phylogeny of *Antennaria* and also in defining its relationship to the outgroup taxa (Bayer, Soltis, & Soltis, in press). Phylogenetic analysis indicates that, relative to the outgroups included, *Antennar-*

EVOLUTIONARY AND PHYTOGEOGRAPHIC TRENDS IN *ANTENNARIA*

POLYPLOID PILLAR COMPLEX

GEYERIAE   ARCUATEAE   ARGENTEAE   DIMORPHAE   PULCHERRIMAE   CATIPES

| Strictly amphimictic, seeds are produced sexually | Both amphimictic and apomictic species occur |

| Diploids 2x = 28 | Diploids to tetraploids 2x = 28 to 4x = 56 | Diploids to dodecaploids 2x = 28 to 12x = 168 |

| Arid habitats at low elevations | Very diverse habitats at many elevations, some are edaphic endemics |

| Sexual dimorphism: poorly evolved ———▶ Strongly evolved |

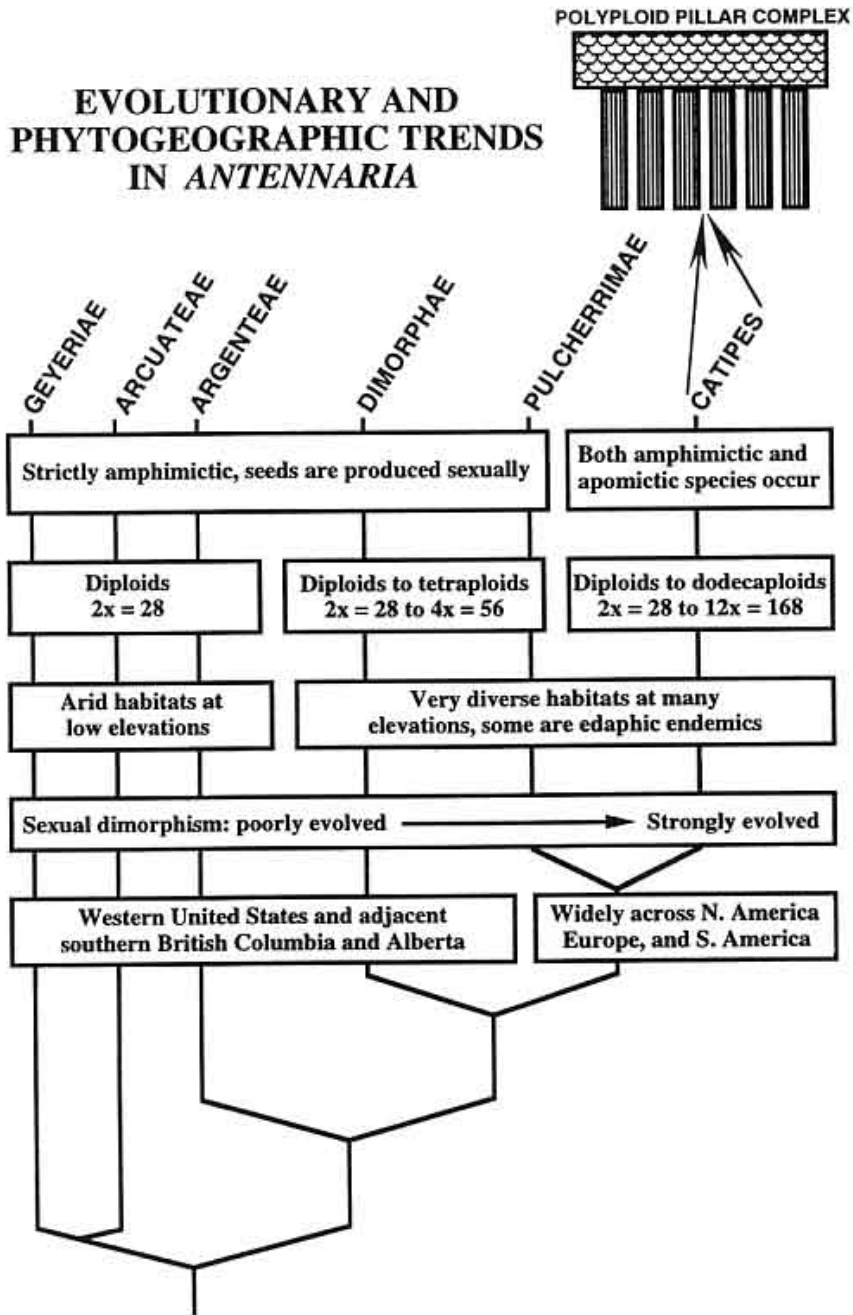| Western United States and adjacent southern British Columbia and Alberta | Widely across N. America Europe, and S. America |

Fig. 1. Evolutionary and phylogenetic trends within the genus *Antennaria* are superimposed on a reduced cladistic analysis based on morphology and DNA sequences from the internal transcribed spacer regions of nuclear ribosomal DNA (ITS). The monotypic groups *Geyeriae* and *Arcuateae* are viewed as the most unspecialized groups within the genus are relatively primitive members of the genus. On the other hand the speciose *Catipes* group is regarded as being the most specialized lineage and it is from this group of sexual diploids that all the polyploid pillar complexes within the genus have been derived.

ia is a well-supported monophyletic group (Bayer, Soltis, & Soltis, in press). Based on the genera surveyed, *Leontopodium* appears to be the sister genus of *Antennaria* (Bayer, Soltis, & Soltis, in press). The general topology of the molecular trees agrees with that based on previous morphological analyses (Bayer 1990a) and indicates that *Antennaria* is composed of six clades of equal rank, corresponding to the traditionally recognized informal groups, the *Geyeriae, Argenteae, Dimorphae, Pulcherrimae, Catipes*, as well as a new group, the *Arcuatae* (Fig. 1). Phylogenetic analysis of ITS sequences (Bayer, Soltis, & Soltis, in press) suggested the placement of *A. arcuata* in its own group, hence six monophyletic clades are recognized instead of the five that were evident in the analysis of morphology (Bayer 1990a).

Phylogenetic trees based on morphology (Bayer 1990a) and ITS sequences (Bayer, Soltis, & Soltis, in press) can be reduced to form a consensus of the six major lineages within the genus (Fig. 1). Evolutionary and phytogeographical features can be superimposed on the tree, which show interesting trends within the genus (Fig. 1). The least specialized groups, the *Geyeriae, Arcuateae*, and *Argenteae* all occur in arid habitats at low elevations in the western United States (Fig. 1). They are all strictly diploid amphimicts in which sexual dimorphism is poorly developed. The *Dimorphae* and *Pulcherrimae* groups show moderate degrees of specialization, in that they are strictly amphimictic diploids to tetraploids and sexual dimorphism is well-developed (Fig. 1). They have expanded their ranges beyond the western United States to other parts of the New and Old Worlds (Fig. 1). The *Catipes* group consists of sexual diploids and tetraploids and derived from them are all of the polyploid agamic complexes in the genus (Fig. 1). Most of the species of the *Catipes* group have aggressive horizontal stolons, an effective means of asexual reproduction, and sexual dimorphism is well developed. Amphimixis, apomixis (agamospermy), and the very high levels of polyploidy (up to dodecaploid; Bayer & Minish 1993) are prevalent among polyploid pillar complexes that are derivatives of the sexual diploid taxa from the *Catipes* lineage (Fig. 1). Five polyploid agamic complexes, *A. alpina* (L.) Gaertn., *A. howellii* E. L. Greene, *A. parlinii* Fern., *A. parvifolia* Nutt., and *A. rosea* E. L. Greene, have evolved via multiple hybridization from among 16 of the 17 members of the *Catipes* group (Bayer 1987a; Bayer, Soltis, & Soltis, in press). The great success of the *Catipes* group seems to be correlated with their ability to grow in a diversity of habitats (many of them are specialized as edaphic endemics, such as *A. virginica* Stebbins on Devonian-age shale barrens (Bayer & Stebbins 1987, 1993), *A. suffrutescens* Greene on serpentine (Bayer & Stebbins 1993), and *A. aromatica* Evert and *A. densifolia* A. E. Porsild on limestone talus (Bayer 1989a)) throughout their range from Great Britain across Eurasia and North America to Tierra del Fuego. It is also due to their acquisition of characters such as strong sexual dimorphism, aggressive vegetative reproduction (stolons), polyploidy, and agamospermy (Fig. 1).

Clearly, one way to comprehend the perplexing patterns of variation found in the agamic complex is to study the extant sexual progenitors of the complex. Once morphological, ecological, and genetic variation in sexual species is delimited then that of the polyploids can be better understood and explained. This is the approach that I have taken in my work with all the polyploid complexes in *Antennaria*. We shall now focus in on the multiple hybrid origin of one of these polyploid agamic complexes, the *A. rosea* complex, which is derived from sexual species of the Catipes groups.

Evolution of the Antennaria rosea polyploid agamic complex

Antennaria rosea is one of the most morphologically diverse polyploid complexes in *Antennaria* (Bayer 1990b). 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, Saskatchewan, to the western shores of Hudson Bay (Bayer 1989b). 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. *Antennaria rosea* appears to occupy a wide variety of habitats from dry steppe to alpine tundra (Fig. 5; Bayer 1990a; Bayer, Purdy & Lebedyk 1991). It is often found sympatric with or in parapatric populations near its sexual relatives (Bayer, Purdy & Lebedyk 1991). Individual clones of *A. rosea* often display suites of morphological characters that are indications of their parentage, as these same features are characteristic of certain sexual taxa (Bayer 1990a; Bayer, Purdy & Lebedyk 1991). Casual field observations indicated that clones of *A. rosea* often resemble the sexual species that occur in habitats that are most similar to their own (Bayer, Purdy & Lebedyk 1991). It is likely that the ecological amplitude of *A. rosea* has perhaps increased over those of its sexual progenitors because the overall genetic composition of the species is more diverse as a result of heterogeneous gene combinations from many divergent sexual species (Bayer, Purdy & Lebedyk 1991). It was not clear whether *A. rosea* occupied only habitats that were very similar to those of its sexual progenitors or whether it sometimes occurred in hybrid, intermediate or unique habitats.

The species has triploid (2n = 42), tetraploid (2n = 56), and pentaploid (2n = 70) cytotypes, but the tetraploids are by far the most common (Bayer & Stebbins 1987). *Antennaria rosea* is a gametophytic apomictic, and because the genus is dioecious, populations of *A. rosea* consist entirely of pistillate clones (Bayer 1987a; Bayer & Stebbins 1987). Taxonomically, I have treated this compilospecies as one large polymorphic species, *A. rosea* s.l., because it is unrealistic to try to recognize all the microspecies that delineate the complex (Bayer 1989c).

I have hypothesized that the variation in the *A. rosea* complex is derived from several sexually reproducing species of *Antennaria* primarily from the southern, unglaciated, portions of the western cordillera (Bayer 1990b). *Antennaria aromatica, A. corymbosa* E. Nelson, *A. pulchella* E. Greene, *A. microphylla* Rydb., *A. racemosa* Hook., and *A. umbrinella* Rydb. are sexual species that appear to be implicated in the parentage of *A. rosea* (Fig. 2). [*Antennaria pulchella* and *A. media* E. L. Greene are a diploid progenitor - polyploid derivative pair of taxa that occur in the cordilleran system of western North America. The sexually reproducing diploid, *A. pulchella*, has a very restricted range, in the subalpine-alpine zones of the southern Sierra Nevada from the area around Lake Tahoe to the Mt. Whitney region. *Antennaria media* is a widespread polyploid that occurs throughout the cordilleran system of western North America from the Mexican border to the subarctic. The combined taxa will be referred to as *A. pulchella/media* in the text.]. Additionally, *A. marginata* E. Greene, and *A. rosulata* Rydb. may have contributed to the genetic composition of the *A. rosea* complex (Fig. 2). *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. pulchella/media*, are more widespread throughout the western Cordillera from the southern portions in New Mexico and California to the Yukon. The ranges of the sexual species, for the most part, overlap completely with that of *A. rosea*. Populations that were surveyed electrophoretically along with maps outlining the distributions of these sexual species can be found in Bayer (1988).

Morphological evidence

It was obvious to me, based on casual herbarium and field observations, that suites of morphological characters that are unique to a particular sexual species often occur in different combinations in the segregates of *A. rosea* (Bayer 1990b). Consequently, *A. rosea* is a com-
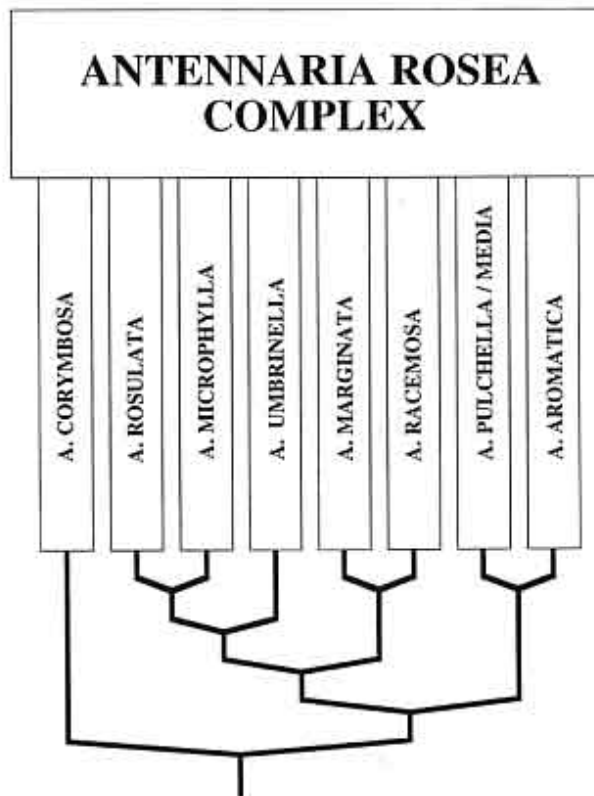

Fig. 2. Reticulate evolution in *Antennaria* and formation of the *A. rosea* polyploid agamic complex. Putative relationship of the *A. rosea* complex to its eight sexual, primarily diploid, progenitors, *A. aromatica, A. corymbosa, A. marginata, A. microphylla, A. pulchella* (tetraploids = *A. media*), *A. racemosa, A. rosulata*, and *A. umbrinella*. Phylogenetic relationships of the sexual diploid species themselves is shown.

pilospecies, having arisen through multiple hybridization and introgression from among several sexual species. In order to test this hypothesis morphological characters were measured on a set of representative specimens of *A. rosea* and its eight putative diploid progenitors (Bayer 1990b). Various ordination and clustering techniques (outlined in Bayer 1990b) were performed and a redrawn version of one of these is shown in Fig. 3. The phenetic analyses (Bayer 1990b) indicated that *A. aromatica, A. corymbosa, A. microphylla, A. pulchella/media*, and *A. umbrinella* are the major sexual progenitors of the *A. rosea* complex (Fig. 3). 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 lack glandular hairs on the upper flowering stem, are more robust and are entirely pistillate (Bayer 1990b). Incidentally, the rose phyllary color in some *A. rosea* clones is not prevalent in any of
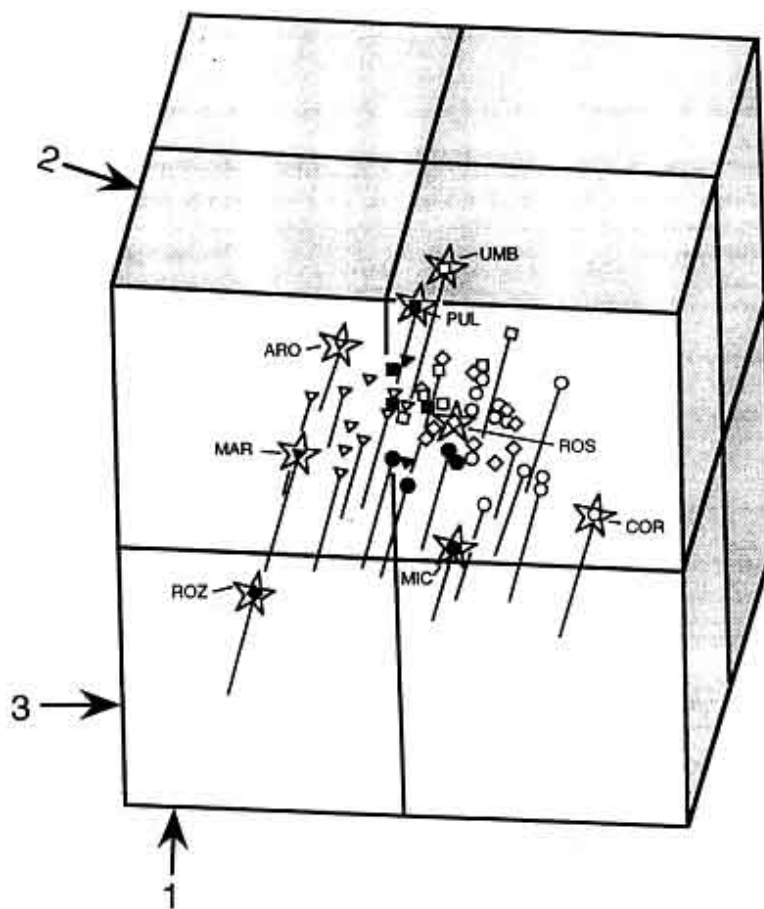
Fig. 3. Three dimensional principal components analysis (PCA) composed of 55 OTUs of Antennaria. Factors 1 to 3 are labelled with arrows. The species composition of the OTUs is one centroid (Stars with specific epithet symbols inside) each of *Antennaria aromatica* (open, downpointing triangles), *A. corymbosa* (open circles), *A. marginata* (closed, downpointing triangles), *A. microphylla* (closed circles), *A. pulchella/media* (closed squares), *A. rosulata* (closed diamonds), and *A. umbrinella* (open squares) and 47 OTUs of *A. rosea* (open diamonds). *Antennaria rosea* OTUs are labelled with the specific epithet symbol of the species to which it has the highest similarity as indicated by Pearson product-moment correlation coefficients. The centroids are labelled as follows: *A. aromatica* (ARO), *A. corymbosa* (COR), *A. marginata* (MAR), *A. microphylla* (MIC), *A. pulchella/media* (PUL), *A. racemosa* (RAC), *A. rosea* (ROS), *A. rosulata* (ROZ), and *A. umbrinella* (UMB). This three-dimensional projection was obtained by rotation of the PCA by the Mac-Spin program (D^2 Software, Austin, Texas); the diagram redrawn from Fig. 2 of Bayer (1990b).

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* (Bayer 1990b). Very few clones of *A. rosea* display morphological characteristics that can be attributed to *A. marginata* or *A. rosulata* (Fig. 3), providing only weak evidence that they may have contributed to the genetic composition of *A. rosea* (Bayer 1990b). The putative sexual progenitors of the *A. parvifolia* polyploid complex include *Antennaria marginata* and *A. rosulata* (Fig. 3; Bayer 1987a).

Antennaria racemosa is a sexual diploid that is morphologically very different from the other sexual species (Bayer 1987b). Consequently, when included in a principal components analysis (PCA) it caused all the operational taxonomic units (OTUs) of the other species to mass together, therefore could not be incorporated into the formal analysis (See Bayer 1987b, p. 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 (Bayer 1990b). *Antennaria racemosa* has large, glabrous basal leaves, an open,

racemose arrangement of heads, and purple stalked glands on its cauline leaves and peduncles (Bayer 1987b). These characters are seen in *A. rosea* segregates that have often been identified as the microspecies *A. alborosea* A. E. Porsild. No other amphimictic species of *Antennaria* has this unique combination of characters, so they must be attributed to parentage involving *A. racemosa* (Bayer 1990b). In summary, morphometric analyses have shown that six sexually reproducing progenitors, *A. aromatica*, *A. corymbosa*, *A. microphylla*, *A. pulchella/media*, *A. racemosa*, and *A. umbrinella* are primary source of morphological variability found in the *A. rosea* complex (Fig. 3). Additionally, two other sexually reproducing species, *A. marginata* and *A. rosulata*, may have donated to the genetic complexity of the *A. rosea* complex (Fig. 3).

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 1990b). Based on morphology, the *A. rosea* polyploid agamic complex is a typical compilospecies,

Genetic Distance

0.10 0.08 0.06 0.04 0.02 0.00

Fig. 4. Distance phenogram (UPGMA) derived from Nei's genetic distances of all pairwise comparisons of 33 populations of *Antennaria rosea* with average identity values for eight sexual species of *Antennaria*, including *A. aromatica* (ARO), *A. corymbosa* (COR), *A. densifolia* (DEN), *A. marginata* (MAR), *A. microphylla* (MIC), *A. pulchella/ media* (PUL), *A. racemosa* (RAC), *A. rosulata* (ROZ), and *A. umbrinella* (UMR). Population designations for the *A. rosea* (ROS) populations are the same as those cited in Tab. 1 of Bayer 1989b. Cophenetic correlation coefficient is 0.7946. The diagram was redrawn from Fig. 2 of Bayer (1989b).
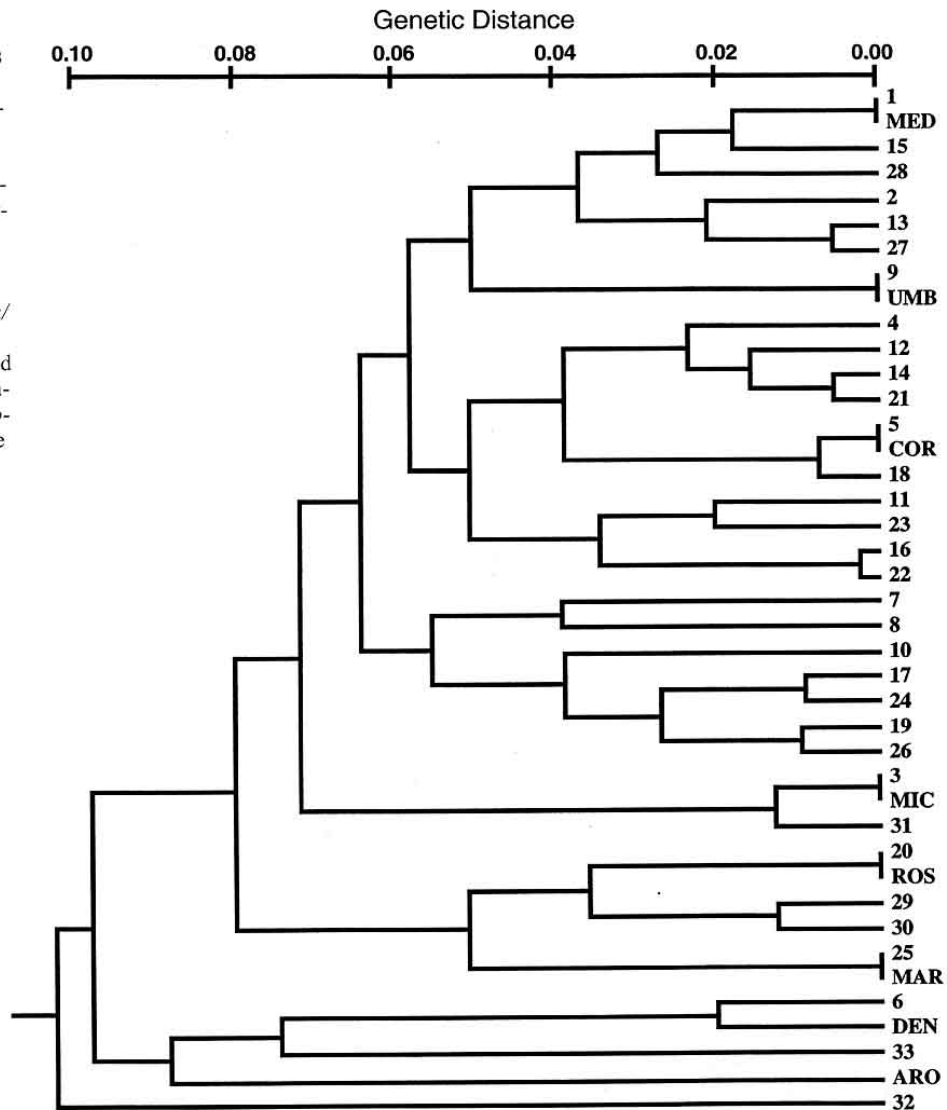
i.e. it is the result of hybridization from among several sexually reproducing diploids and tetraploids.

Isozyme evidence

Isozymes have been shown to be useful not only in looking at divergence among populations of plants, but also in looking at the origins of diploids and polyploids of hybrid origin (Crawford 1983, 1985). With regard to the *Antennaria rosea* complex, isozymes have been used to look at divergence among the diploid progenitors of the complex (Bayer 1988, 1989d), clonal diversity in *A. rosea* (Bayer 1990c, 1991) and the origins of the *A. rosea* complex (Bayer 1989b).

Morphological differences among the sexual species,

such as those in *Antennaria*, 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 comparable to that occurring in other genera such as *Quercus* (Manos & Fairbrothers 1987), and *Heuchera* (Saxifragaceae; Soltis 1985) in which only moderate amounts of divergence have occurred at the enzyme loci, whereas relatively large amounts of morphological divergence has taken place among the species.

As would be expected for intraspecific comparisons, average values of genetic identities, 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

(Bayer 1989b). The cluster analysis (UPGMA) of the genetic distance matrix of 33 *A. rosea* populations and eight populations representing taxa that are related to *A. rosea* (Fig. 4) effectively portrays the relationship of the populations and species (Bayer 1989b). Most of the *A. rosea* populations are most similar to populations of *A. corymbosa*, *A. microphylla*, *A. pulchella/media* and *A. umbrinella*, whereas fewer populations are similar to *A. aromatica*, *A. marginata*, and *A. rosulata* (Fig. 4; Bayer 1989b). The segregates of *A. rosea* should contain alleles that have their origins in the sexual taxa (Fig. 2), however only *A. corymbosa*, *A. microphylla*, and *A. umbrinella* have alleles that are unique (Bayer 1989b). 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* (Bayer 1989b). Values of genetic identity (I) indicate that although the remaining species, *A. aromatica*, *A. marginata*, *A. pulchella/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 markers (Bayer 1989b). Similar results, where unique alleles of a few sexual progenitors could be used as independent evidence to substantiate the genomic composition of polyploids, were obtained (Bayer & Crawford 1986) for the *A. parlinii* and *A. howellii* (previously *A. neodioica* Greene) complexes.

Antennaria rosea probably arose fairly recently in the Rocky Mountains of the western United States because this is the region where it is still sympatric with its diploid progenitors (Bayer 1989b). This is also supported by the fact that the only novel allele (Pgm-1ᵃ) found in *A. rosea* has not been detected in the probable sexual progenitors (Bayer 1989b). It would be likely that if sufficient time would have elapsed such that more unique alleles would be found in the *A. rosea* complex, then the polyploids would be relatively old (Bayer 1989b). Similar results have been found in other relatively youthful polyploids, as *Tragopogon* (Roose & Gottlieb 1976).

In additional studies of the *A. rosea* complex (Bayer 1990c; Bayer 1991) the clonal diversity in populations within the complex were studied to look at the distribution and number of clones in those populations. Clonal diversity among 63 populations of *A. rosea* was studied over a large portion of its range (Bayer 1990c). Isozyme electrophoresis utilizing four polymorphic enzyme systems detected 192 multilocus genotypes among the populations (Bayer 1990c). Populations of *A. rosea* tend to be composed of one or a few genotypes (range 1 - 11; mean 3.5), and these genotypes usually occur in only one or a few localized populations (Bayer 1990c). Geographic patterns of clonal diversity may be a result of frequent genesis of new clones in populations that occur in areas where sexual relatives of *A. rosea* donate compatible pollen to facultatively sexual apomicts. Populations from previously glaciated regions tend to have fewer clones per population than those from unglaciated portions of the range. However, the evolution of new apomictic clones in *A. rosea* is paradoxical. If *A. rosea* is obligately agamospermous, then how do new clones arise? Perhaps some clones of *A. rosea* occasionally produce sexual embryo sacs (facultative sexuality) and these are subsequently fertilized by compatible pollen from nearby sexual progenitors (Bayer 1990c). As mentioned above, unique marker allozymes are supportive of the fact that *A. corymbosa*, *A. microphylla*, and *A. umbrinella* are among the parents of the *A. rosea* complex (Bayer 1989b). Fourteen of the 17 populations of *A. rosea* containing clones that have these unique alleles are from sites that overlap the range of the particular sexual species containing the same marker alleles, which further strengthens this argument (Bayer 1990c). Geographic patterns of clonal diversity in *A. rosea* may be a result of more frequent genesis of new clones in populations that co-occur in areas where sexual relatives of *A. rosea* contribute large amounts of compatible pollen to facultatively sexual clones (Bayer 1990c). Clausen's "Henry Ford" or "model T" hypothesis (Clausen 1954; Marshall & Brown 1981) concerning the adaptive significance of apomixis may apply to the case of *A. rosea*, where facultative sexuality continually supplies the necessary genotypes to be tested, but only the most successful ones are "reproduced authentically" and continuously via apomixis. Facultative amphimicts may play a very important role in the maintenance of clonal diversity in the *A. rosea* complex (Bayer 1990c).

This study (Bayer 1990c) also showed that clonal diversity declines with distance from the center of distribution.Lower numbers of apomicts in populations at the margins of the ranges could have several possible causes. First, these populations could be more recently established. Secondly, populations near the center of the range, where the largest numbers of sexual species occur, could be more clonally diverse because new apomicts arise more frequently as a result of facultative sexuality in some clones of *A. rosea* (Bayer 1990c). This might also account for the sporadic occurrence of staminate *A. rosea* plants near the center of the range (Bayer, unpubl. obs.). Also, pistillate triploid *A. rosea* occurs mostly near the center of the range of the species (Bayer 1987a; Bayer & Stebbins 1987; Bayer 1990c). Finally, even if rates of genesis of new apomicts are the same, populations in the center of the range could be more diverse if selection in these regions is less intense. Habitat differences and availability over the entire range of the species also perhaps play a part in influencing clonal diversity in central vs. marginal populations of *A. rosea*, as the diversity of habitats suitable for *A. rosea*

seem to decrease on margins of its range (Bayer, pers. obs.). Consequently, stronger directional selection in marginal sites along with balanced selection in central sites perhaps accounts for the observed patterns of clonal diversity. Although genetic drift can not be discounted as playing a large role in influencing the numbers of clones in marginal populations, it seems unlikely as these populations tend to be of equal size to most central populations (Bayer, pers. obs.).

The results of these studies (Bayer 1990c; Bayer 1991) also support morphological data (Bayer 1990b) indicating that *A. rosea* is a species complex composed of numerous apomicts. It is difficult to account for this clonal diversity because *A. rosea* is a gametophytic apomict and almost entirely pistillate. If *A. rosea* is an obligate apomict, then the diversity could only arise from mutations or from many independent origins. It seems unlikely that mutations could account for the large numbers of clones that have been encountered, because a previous study has demonstrated that only one Pgm-1 allele occurs in *A. rosea* that has not also been detected in its sexual progenitors (Bayer 1989b). If *A. rosea* is facultatively sexual, then when it comes in contact with compatible pollen donors, new apomicts might arise through sexual reproduction.

In summary, isozymes were useful in documenting the origins of the *A. rosea* complex from among several diploids, including *A. corymbosa*, *A. microphylla*, and *A. umbrinella* (Fig. 2), but could neither confirm nor discount the others as ancestors of the complex. It is likely that *A. rosea* is a facultative apomict and that new clones are being continually introduced into the environment by hybridization back to their sexual progenitors. These new apomictic clones are then tested by natural selection.

Ecological evidence

Based on informal field observations, each of the eight sexual progenitor species that may have given rise to the *Antennaria rosea* complex (Fig. 2) appears to be associated with rather specific habitats (Bayer 1987a). For example, in west-central Montana up to six species, *A. aromatica*, *A. corymbosa*, *A. media*, *A. microphylla*, *A. racemosa*, and *A. umbrinella*, can occur on a single mountain (Fig. 5), but each appears to be associated with a different community (Bayer 1987a). *Antennaria microphylla* typically grows at the lower elevations along river terraces with sagebrush, whereas *A. umbrinella* is usually found at drier sites with sagebrush or Ponderosa pine (Fig. 5; Bayer 1987a; Bayer, Purdy, & Lebedyk 1991). The montane zone in the understorey of moist coniferous forests is the typical habitat of *A. racemosa* (Fig. 5; Bayer 1987a; 1990b). Both *A. aromatica* and *A.*
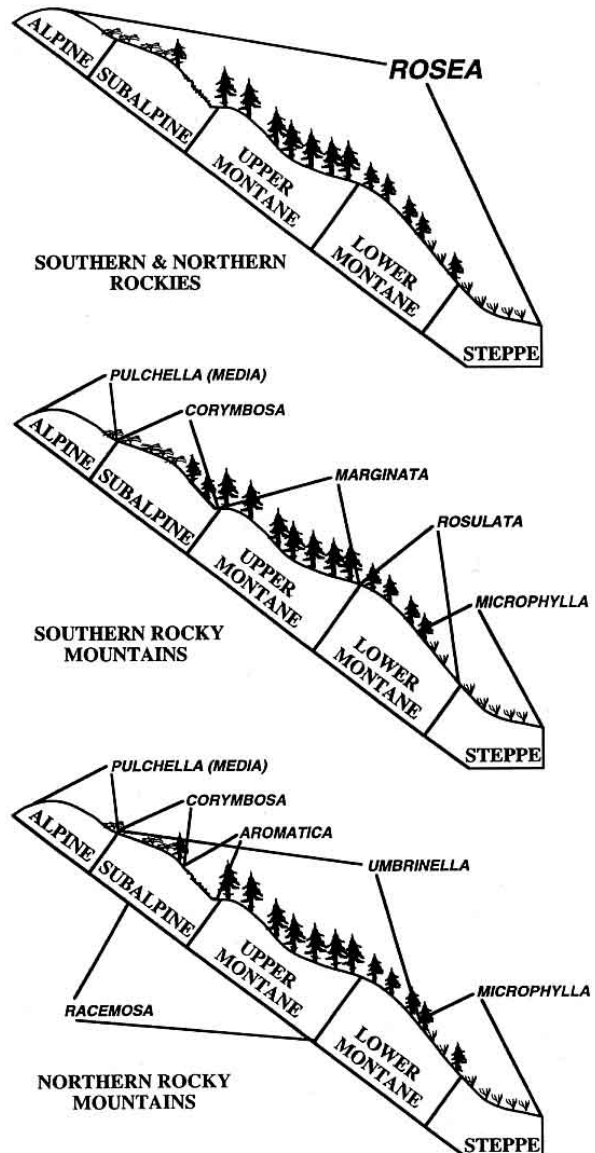

Fig. 5. Mountain slopes in the southern and northern Rocky Mountains of western North America. The boundary between the northern and southern Rockies is the Red Desert in southwestern Wyoming, U.S.A. On the slopes, alpine above treeline is gradually replaced by subalpine krummholz, followed by montane coniferous forests, and finally by pine savannah and sagebrush steppe at the lowest elevations. The relative elevational / ecological distribution of *Antennaria rosea* and each of its eight sexual, primarily diploid, progenitors, *A. aromatica*, *A. corymbosa*, *A. marginata*, *A. microphylla*, *A. pulchella* (tetraploids = *A. media*), *A. racemosa*, *A. rosulata*, and *A. umbrinella*, is indicated on the slopes. Species are labelled with their specific epithets.

corymbosa occur at timberline and marginally in the alpine, but the former is associated with limestone talus, while the latter is found in moist *Salix* thickets (Fig. 5; Bayer 1987a; 1990b). *Antennaria media* is found on dry, alpine tundra (Fig. 5; Bayer 1990d; Bayer, Ritland, & Purdy 1990). In the southern Rockies, *A. marginata* and *A. rosulata* also appear to occupy distinct habitats (Fig. 5; Bayer, Purdy & Lebedyk 1991). Sexual populations appear to be reproductively isolated by ecological mechanisms and as a result when two species grow in close proximity hybrids often occur (Bayer 1987a; Bayer, Purdy & Lebedyk 1991).

As a part of a community, a plant population occupies a niche, an environment composed of both biotic and abiotic elements, both of which must be evaluated to acquire a complete understanding of a species' habitat and niche. One purpose of the ecological study (Bayer, Purdy & Lebedyk 1991) of *A. rosea* and its progenitors was to investigate and quantify the habitat diversity in *A. rosea* and its sexual progenitors to determine whether the individual taxa are ecologically distinct. The need for studies of the adaptive significance of polyploidy, using modern statistical analyses of plant community association has been underscored by both Stebbins (1984) and Ehrendorfer (1980) and the ecological study (Bayer, Purdy & Lebedyk 1991) endeavored to contribute to our knowledge on that topic.

In this study (Bayer, Purdy & Lebedyk 1991) environmental and relative abundance of community associate at sites occupied by *A. rosea* and its putative progenitors were surveyed. Ordination of species and environmental variables from the 101 study sites was carried out using the canonical correspondence analysis (CCA) option of the Canonical Community Ordination (CANOCO) program (ter Braak 1985). This method of analysis allows the environmental variables to be related to species data simultaneously and is becoming the preferred ordination method for the analysis of data used in vegetation classification (ter Braak 1986, 1987, 1988). The CANOCO ordination arranges sites such that those occupying similar habitats appear in close proximity to each other. Each of the sexual species of *Antennaria*, including *A. aromatica, A. corymbosa, A. marginata, A. media/pulchella, A. microphylla, A. racemosa, A. rosulata*, and *A. umbrinella*, appears to occur in a distinct habitat (Bayer, Purdy & Lebedyk 1991). Both community associates (the biotic factors) and environmental variables (the abiotic factors) can be used to predict which *Antennaria* species will occur in a given habitat and vice-versa (Bayer, Purdy & Lebedyk 1991). In most cases, several variables can be used to accurately and effectively describe the habitat, although many of the species habitats can be confidently distinguished from those of the other *Antennaria* species by the use of single variables (Bayer, Purdy & Lebedyk

1991). For example, all *A. aromatica* sites are characterized by having soils with amounts of $CaCO_3$ that are several orders of magnitude higher than those of any other site (Bayer, Purdy & Lebedyk 1991).

Some sympatric species pairs have similar habitats, although spatially overlapping or conterminous ones are uncommon (Bayer, Purdy & Lebedyk 1991). The CCA indicates that the habitats of the following sympatric species pairs are the most likely to overlap: *A. corymbosa - A. microphylla, A. corymbosa - A. media, A. microphylla - A. umbrinella*, and *A. media - A. umbrinella* (Bayer, Purdy & Lebedyk 1991). These occur because very different mountain habitats can often occur side by side (Bayer, Purdy & Lebedyk 1991). Mountain stream beds running through a surrounding terrain that is by comparison very dry creates the situation where two very different communities exist juxtaposed (Bayer, Purdy & Lebedyk 1991). For example, both *A. microphylla* and *A. umbrinella* occur at similar elevations, but the habitat of *A. microphylla* is floodplains or moist alkaline depressions, while that of *A. umbrinella* are the drier sagebrush covered hillsides (Bayer, Purdy & Lebedyk 1991). In ecotonal areas the two species can co-occur such as in the Flint Mountains, Granite Co., Montana (See Bayer et al. MT-736/MT-738 at ALTA) (Bayer, Purdy & Lebedyk 1991). On the other hand, hybridizations are a necessary step in the evolution of polyploid agamic complexes. Interspecific F_1 hybrids are frequently found in communities where two or more sexual species occur sympatrically (Bayer 1987a). Such hybrids are usually easy to identify because they are morphologically intermediate between their parents (Bayer 1987a). However, later generation backcross progeny and introgressant segregates may be very difficult or impossible to distinguish morphologically from their recurrent parent (Bayer 1987a). Later generation hybrids become polyploidized and acquire agamospermy becoming the fully fertile agamic microspecies, which make up the large polyploid agamic complexes such as *A. rosea* (Bayer 1987a).

Habitat divergence tends to follow morphological divergence among the sexual taxa, which was discussed above (Bayer 1987a). Those taxa that tend to be morphologically most distinct, such as *A. racemosa* and *A. marginata*, are also ecologically discrete (Bayer, Purdy & Lebedyk 1991). Morphometrics indicated that *A. aromatica, A. media/pulchella*, and *A. umbrinella* have the most similar morphologies and introgressive hybridization is strongly indicated in some populations (Bayer 1987b). *Antennaria aromatica* however is very distinct ecologically (Fig. 5) from *A. media* and *A. umbrinella* and the last two also occupy rather discrete habitats (Bayer, Purdy & Lebedyk 1991). Habitat divergence among the species has obviously played an important role in the evolution of these species, as was suggested

earlier by Bayer (1987a). Ecological isolation along with geographic isolation are the primary isolating mechanisms that help maintain species integrity and allow the species to continue to diverge (Bayer, Purdy & Lebedyk 1991).

The *A. rosea* sites occupy ordination space on the diagram (see Bayer, Purdy & Lebedyk (1991, Figs 5-7) that lies in the center of the ordination and overlaps at least parts of those of all the sexual species except *A. aromatica* and *A. racemosa* (Bayer, Purdy & Lebedyk 1991). Several sites are however close to some of the A. aromatica sites (Bayer, Purdy & Lebedyk 1991). Many *A. rosea* sites do not occur in distinct habitats themselves, but instead occupy habitats that are very similar to those of their sexual progenitors (Bayer, Purdy & Lebedyk 1991). Some sites do however fall in between the groups of sites of the sexual species and these habitats could be described as hybrid habitats since they have sets of conditions that are intermediate between or among groups of sexual taxa, as is indicated by CCA (Bayer, Purdy & Lebedyk 1991). None of the *A. rosea* sites cover the range of abiotic conditions associated with the sexual taxa, i.e. they don't completely overlap the habitat of any of their sexual relatives (Bayer, Purdy & Lebedyk 1991). The CCA supports the hypothesis for the multiple hybrid origin of *A. rosea* proposed in Bayer (1990a), in that many sites of *A. rosea* occupy similar habitats to their diploid progenitors, while others seem to occupy hybrid habitats that are intermediate between those of their sexual progenitors (Bayer, Purdy & Lebedyk 1991). The greatest amount of overlap between sites of *A. rosea* and those of the sexual progenitors occurs between *A. rosea* and *A. microphylla* and *A. umbrinella* and to a lesser degree *A. corymbosa, A. marginata, A. media,* and *A. rosulata* (Bayer, Purdy & Lebedyk 1991).

What are the evolutionary implications of habitat divergence in relationship to allopolyploidy? Several authors have pointed out that the pivotal studies that may lead us to learn more about the adaptive significance of polyploidy may be ecological studies of diploids and their polyploid derivatives. A need for the extension of studies of the adaptive significance of polyploidy, using modern statistical analyses of plant community associations, particularly in closely related diploids and polyploids, has been stressed in reviews by both Stebbins (1984) and Ehrendorfer (1980). Fowler & Levin (1984) stress the importance of ecological factors, especially habitat divergence, in establishment and persistence of polyploids. Stebbins (1984) has commended the studies of Johnson & Packer (1965, 1967, 1968) that emphasize the significance of ecological factors in delimiting the relative distribution of diploids and polyploids.

The "secondary contact hypothesis" (Stebbins 1984, 1985) places importance on secondary contact and sub-

sequent hybridization between differentiated diploids to produce new, highly adaptive gene combinations which are subsequently maintained through polyploidy (and in the case of *A. rosea*, agamospermy). Stebbins (1984) predicted that this secondary contact might happen most often during glacial episodes when populations of well differentiated diploids would be brought together as the result of the shifting of communities because of changing climatic conditions. In the *A. rosea* complex the situation is more complicated than in many other polyploid complexes because several progenitor species, including *A. aromatica, A. marginata, A. pulchella,* and *A. umbrinella,* have sexual autopolyploid cytotypes in addition to sexual diploids. Hybridization among all the cytotypes has led to an enormous amount of variation in morphology among the descendent *A. rosea* clones. The study of the ecology of *A rosea* and its sexual relatives (Bayer, Purdy & Lebedyk 1991) illustrates that it is possible for the *Antennaria* species to come into contact to hybridize because their habitats overlap sporadically.

Ehrendorfer (1980) has emphasized the fact that in young allopolyploid complexes, the polyploid derivatives generally occupy habitats that are different from their progenitors. Using examples from two genera, *Cruciata* (Rubiaceae) and *Knautia* (Dipsacaceae), he contended that in these genera, the diploids are morphologically uniform and ecologically separated (Ehrendorfer 1980). The polyploid derivatives are morphologically diverse and occupy different habitats than their progenitors. He also asserts that the polyploids in these genera do not occur in environments that are more harsh than those occupied by their diploid ancestors, in fact they seem to occupy less extreme environments (Ehrendorfer 1980). Stebbins (1985) has also rejected the hypothesis that polyploids succeed because they have a superior tolerance of harsh ecological or climatic conditions. The results of the ecological study of habitat differentiation among species of *Antennaria* (Bayer, Purdy & Lebedyk 1991) supports these hypotheses, in that well over half of the *A. rosea* sites occupy habitats not occupied by their progenitors and also the habitats would seem to be moderate in comparison to those occupied by many of the sites of the progenitors, which seem to occupy more extreme sites with regard to a host of environmental parameters. Levin's conclusion that polyploidy may drive a population into a new "adaptive sphere", and allow it to occupy habitats that are beyond that of its progenitors (Levin 1983) is supported by the results of this investigation. Polyploidy, particularly when accompanied by hybridization between either different species or different ecotypes of the same taxon, is one of the quickest ways for new species or races to become adapted to different ecological circumstances (Stebbins 1984).

Ehrendorfer (1980) has suggested that in established

floras polyploidy contributes intermediate "fill-in" taxa that contribute to a more intensive partitioning of areas and eventually leads to a saturation of most available habitats by the progenitor taxa and their polyploid derivatives. This may be the most adaptively significant role that polyploids perform. *Antennaria rosea* seems to fulfil this prediction in that many of the *A. rosea* populations exist in habitats that are both unoccupied by and intermediate to those of its progenitors. Populations of *A. rosea* can therefore exist parapatrically with those if its progenitors. The idea that habitat differentiation increases the probability of the coexistence of diploids and their polyploid derivatives (Fowler & Levin 1984) is therefore supported by this study. It would be interesting to investigate other polyploid agamic complexes in *Antennaria*, such as *A. alpina*, for similar patterns of habitat differentiation among related amphimictic taxa and their polyploid derivatives.

Conclusions

Antennaria rosea is a model system for studying the evolution of polyploid agamic complexes and it closely follows the outline of the evolution of the typical complex that I presented at the beginning of this paper. Much is known about various aspects of the complex from its origin to the genetic structure of its populations, but much is still to be uncovered. All of the analyses support the relationship of the polyploid *A. rosea* to the diploids *A. aromatica, A. corymbosa, A. marginata, A. microphylla, A. pulchella, A. racemosa, A. rosulata,* and *A. umbrinella*. From a genetic and morphological point of view, *A. rosea* can be described as those segregates that are primarily tetraploid, contain genes from *A. aromatica, A. corymbosa, A. marginata, A. microphylla, A. pulchella/media, A. racemosa, A. rosulata,* and *A. umbrinella*, and have morphological characteristics that can be attributed to one or more of the eight diploids (Fig. 3). The *A. rosea* agamic complex can be considered to be in a mature stage of development because the sexual diploids are still extant, sexual reproduction is evidently still prevalent among many of the facultative apomicts, and there are a large number of widely distributed agamospecies.

The most perplexing problem when considering the taxonomy of the polyploid agamic complexes in *Antennaria* is their apparently limitless amount of morphological variation, compared to that found in the sexual diploid species. In addition to variation in morphological characters, there is considerable variation in ploidy levels and mode of reproduction. If the basis for this variation is determined, then the patterns of variation become comprehensible. The source of the morphological variation in the *Antennaria* polyploids resides with their sexual diploid and tetraploid ancestors (Fig. 2). Consequently, the sexual species must first be delimited and studied before the variation within the polyploid agamic complexes can be explained and circumscribed.

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