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Evolution and Phylogenetic Relationships of the *Antennaria* (Asteraceae: Inuleae) Polyploid Agamic Complexes

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With 5 Figures

Abstract

Antennaria 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 phenomena of polyploidy and agamospermy are prevalent in a large number of the species and this subsequently has led to a great deal of taxonomic confusion. About seventeen species are primarily sexual and diploid (2n = 28). These species are morphologically well-defined and usually have rather restricted geographic ranges that are principally in unglaciated regions. The sexuals appear to be isolated chiefly by environmental and spatial isolating mechanisms as reproductive mechanisms appear to be poorly evolved. Consequently, when two or more sexual species of the same ploidy level co-occur, hybrid swarms may be generated.

The five polyploid complexes differ considerably from one another with respect to ploidy levels, morphological variation, and reproductive modes. The polyploid levels in *Antennaria* range from tetraploid (2n = 56) to decaploid (2n = 140). The polyploid complexes generally have wider geographic ranges and possibly greater ecological amplitudes than the diploids and this is possibly the result of their diverse genetic composition. Sexual polyploid populations usually occur in southern (unglaciated) areas, whereas the asexual polyploid populations of the same species are found in northern (glaciated) regions. Agamospermy in *Antennaria* is always associated with polyploidy, but not necessarily vice versa.

The polyploid complexes are the result of multiple hybrid origin from among the sexual diploid species. The agamic complexes may be morphologically confluent with one another because they share sexual progenitors. The diploids give rise to polyploids through the processes of interspecific hybridization and backcrossing among themselves and probably through hybridization with facultatively sexual apomicts. The *Antennaria* agamic complexes can be considered to be in a mature stage of development (sensu GRANT, 1981) because the sexual diploids are still extant, sexual reproduction is still prevalent among many of the polyploids, and there are a large number of widely distributed agamospecies.

Introduction

Investigations into the evolution of polyploid agamic complexes represent considerable challenges to evolutionary botanists. Groups such as *Antennaria, Bouteloua, Citrus, 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* (Asteraceae) is a genus which has several interesting features such as gametophytic apomixis, polyploidy, and sexual dioecism, as well as possessing easily accessed centers of diversity, making it an ideal tool to use when studying the evolution of polyploid agamic complexes. About 400 species of *Antennaria* have been described world-wide because past practice has been to afford taxonomic status to each microspecies. This has led to unwieldy taxonomic classifications, which only a few experts on each group can use. Additionally, these types of classifications reveal little about the evolutionary relationships or phylogenies of the agamic complexes. Clearly, the only way to study the evolution of agamic complexes is through a careful series of investigations including morphology, cytology, cytogenetics, phytogeography, ecology, and biochemistry (including enzyme electrophoresis and CpDNA and rDNA restriction site analyses). Some groups have been investigated using a few of these methodologies, but *Antennaria* has been largely neglected until recently renewed interest (Bayer and Stebbins, 1981). This review summarizes our present knowledge of the *Antennaria* agamic complexes and identifies future areas for investigation.

Evolution of the typical 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 an enormous 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 between different microspecies is slightly discontinuous because of their reproductive isolation. Some clones tend to blend morphologically into their sexual relatives, especially if they have a predominance 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 transferred, 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 perfectly well via agamospermy and therefore any hybrid has the potential to become fertile. The preceding general description applys very well to the situation in *Antennaria* as it is currently known. A very useful diagram illustrating most of these general points was first devised by Babcock and Stebbins (1938) and has been reproduced in textbooks by Grant (1981), Dobzhansky et al. (1977) and others and is the basis for figures 1–4.

Historical development

One of the first investigations into the cytological development of an asexual embryo in plants involved Juel's (1898, 1900) characterization of the cytological development of the asexual embryo in *Antennaria alpina* (L.) Gaertner. He found that the embryo arose through the parthenogenetic development of an archesporial (embryo sac mother) cell. This became known as the *"Antennaria"* type of gametophytic apomixis, i.e. diplospory followed by diploid parthenogenesis using current terminology (Grant, 1981). From a developmental viewpoint, this is one of the simplest types of agamospermy. Later, Stebbins (1932b), showed that the same type of agamospermic development was present in several species of the eastern United States, members of the *A. neodioica* Greene and *A. parlinii* Fern. agamic complexes (*sensu* Bayer and Stebbins, 1982).

URBANSKA (1974) has confirmed the pattern for additional species in the *A. alpina* complex.
JUEL (1900) was also the first to suggest that the agamospermous segregates were of hybrid origin. He reasoned that because rare staminate individuals of *A. alpina* were sterile the species must be of hybrid origin because other interspecific hybrids were often sterile. He suggested that *A. alpina* was the result of hybridization between two sexual diploids, *A. dioica* (L.) Gaertner and *A. monocephala* DC. STEBBINS (1932a, b) correctly predicted that members of the *A. parlinii* and *A. neodioica* complexes were probably the result of hybridization among the diploids *A. neglecta* Greene, *A. plantaginifolia* (L.) Hook. and *A. solitaria* Rydb. More recent studies showed that *A. racemosa* Hook. and *A. virginica* Stebb. (figure 1) are also included as sexual ancestors of these complexes (BAYER, 1985a, 1985b).
Early taxonomic work in *Antennaria*, notably that of CRONQUIST (1945, 1950), EKMAN (1927), FERNALD (1898, 1899, 1914, 1924, 1933, 1945), GREENE (1897, 1911, 1912), MALTE (1934), D. NELSON (1899, 1901, 1902), A.E. PORSILD (1950, 1965), M.P. PORSILD (1915, 1931), and RYDBERG (1897) was restricted to new species descriptions (350 for North America) and floristic treatments at an alpha-taxonomic level. A taxonomic monograph of the entire genus has never been attempted. More recently, researchers have used additional methods such as numerical taxonomy (BEALS, 1968), secondary chemistry (DOUGLAS et al., 1977), cytology (BERGMAN, 1951; NYGREN, 1950; URBANSKA 1959, 1961, 1962a, b, 1967a, b, 1968a, b, 1969, 1970, 1983a, b), and quantitative genetics (VON UBISCH, 1930, 1932, 1936). URBANSKA has conducted considerable research on section Carpaticae, which has some polyploidy, but is composed primarily of sexually reproducing plants (URBANSKA, 1959, 1961, 1962a, b, 1967a, b, 1968a, b, 1969, 1970, 1983a, b).

Included and excluded taxa

Antennaria Gaertner is a moderate-sized genus of about 40 species and belongs to the tribe Inuleae (subtribe Gnaphalinae) of the Asteraceae. It is an unusual member of the Inuleae not only because of the predominance of features such as agamospermy, polyploidy and sexual dioecism, but also in its distribution. Most Inuleae occur in southern Africa and Australia (see MERXMÜLLER et al., 1977 for review of the Inuleae), whereas *Antennaria* is restricted to the northern hemisphere, especially N. America, with several unstudied taxa from the Andes of S. America (CABRERA, 1957). *Antennaria* is not the only understudied member of the Inuleae, as MERXMÜLLER et al. (1977) pointed out: "The most surprising fact is the nearly absolute lack of biosystematic studies in the whole tribe."
Antennaria are dioecious, herbaceous perennials with simple, ± woolly, entire basal leaves and ± reduced cauline leaves. Stolons may be present or absent. The flowering stalks are composed of one to many capitula arranged in a ± condensed corymb or raceme (sometimes solitary). The capitula are sexually dimorphic. The phyllaries, imbricated in several series, are dry and scarious, white or more often colored. The involucral bracts of the pistillate plants are lanceolate, whereas those of the staminate are usually broad and petaloid. The florets are numerous, narrowly tubular in the pistillate heads, broadly vasiform in the staminate. The pappus bristles are in a single series, capillary in the pistillate florets, but clavate in the staminate. *Antennaria*, from the Latin *(Antenna)*, because the apically thickened (clavate) pappus bristles of the staminate florets resemble the antennae of certain insects. The species occur in a diverse variety of habitat types from dry desert steppe (*A dimorpha* [Nutt.] Torr. and Gray) to deciduous forest *(A solitaria)* and moist arctic tundra *A. monocephala)*.
The base chromosome number in *Antennaria* is x = 14. Species with 2n = 28 have been considered by North American authors (STEBBINS, 1932a; BAYER and STEBBINS, 1981; BAYER, 1984; CHINNAPPA, 1984, 1986; BAYER and STEBBINS, 1987) to be diploids because no species with somatic numbers lower than 28 have ever been found even among the morphologically most primitive species.
European authors (GUSTAFSSON, 1947; URBANSKA, 1983a, b) consider species with 2n = 28 as tetraploids because in the sister genus of *Antennaria, Gnaphalium* L., species with 2n = 14 are known. In actuality, the *Antennaria* species with 2n = 28 are probably paleopolyploids (sensu EHRENDORFER, 1977), very ancient polyploids that function as diploids (BAYER and STEBBINS, 1987). Their behavior is similar to that of diploids in other groups such as *Crepis* and *Taraxacum* in that the lowest ploidy

levels (i. e. diploids) are always sexually reproducing (BABCOCK and STEBBINS, 1938; RICHARDS, 1973). Additionally, with respect to geographic range morphological variation, and relationships to the higher ploidy levels, they function as "typical" sexual diploids.

Antennaria can be divided into two large groups of species: (group 1) those with well developed polyploidy (up to decaploid) and agamospermy and (group 2) those in which reproduction is sexual and polyploidy has evolved only to the lower ploidy levels. Obviously, it is the former group of species that is more interesting from the perspective of evolution of agamic complexes and will be the focus of attention in this paper.

Five large polyploid agamic complexes (figure 1) are currently recognized as belonging to group 1: *A. alpina* s.l., *A. neodioica* s.l., *A. parvifolia* s.l., *A. parlinii* s.l., and *A. rosea* s.l. (BAYER and STEBBINS, 1987). Each of the complexes contains many previously recognized taxonomic microspecies, but only two, *A. neodioica* and *A. parlinii* have been formally revised taxonomically (BAYER and STEBBINS, 1982). Ploidy levels in the polyploids range from tetraploid (2n = 56) up to decaploid (2n = 140). *Antennaria rosea* Greene and associated sexual taxa have been studied (BAYER, in press a, b), but *A. alpina* and *A. parvifolia* Nutt. await analysis. Sexual taxa that are related to the agamic complexes are numerous (figure 1) and include *A. aromatica* Evert, *A. corymbosa* E. Nelson, *A. dioica, A. friesiana* (Trautv.) Ekman subsp. *alaskana* (Trautv.) Hultèn, *A. marginata* Greene, *A. media* Greene, *A. microphylla* Rydb., *A. monocephala, A. neglecta, A. nordhagiana* Rüne and Ronning, *A. plantaginifolia, A. racemosa, A. rosulata* Rydb., *A. solitaria, A. umbrinella* Rydb., and *A. virginica* (Bayer and Stebbins, 1987). *A. densifolia* Porsild, which occurs in a remote area of the western Canadian arctic, may also belong to this group of species (G. L. STEBBINS, unpubl. obs.).

Those species from group 2 (not discussed elsewhere in this review) should be mentioned briefly. They include the groups outlined by BAYER and STEBBINS (1987) as "carpatica" (including *A. anaphaloides* Rydb., *A. carpatica* (Wahlb.) Bl. and Fingerh. s.str., *A. eucosma* Fern. and Wieg., *A. lanata* (Hook.) Greene, *A. pulcherrima* (Hook.) Greene, and *A. villifera* Borissova), "luzuloides" (consisting of *A. argentea* Benth., *A. luzuloides* Torr. and Gray, and *A. stenophylla* (Gray), and "arcuata", "dimorpha", "flagellaris", "geyeri", and "suffrutescens" (each containing only one species *A. arcuata* Cronq., *A. dimorpha, A. flagellaris* (Gray) Gray, *A. geyeri* Gray, and *A. suffrutescens* Greene, respectively). These non-stoloniferous species are amphimictic and polyploidy, when present, is only developed to the tetraploid level (BAYER and STEBBINS, 1987). The taxonomy of these species is fairly straightforward, as the most intricate pattern of variation is similar to what is found in typical sexual polyploid complexes. URBANSKA (1983a, b; 1985) has analyzed the *A. carpatica* s.l. complex from an ecological aspect, but her final taxonomic synopsis is still forthcoming (K. URBANSKA, pers. com.).

Distribution of sexual species and agamic complexes

The greatest diversity in *Antennaria* is in the Rocky Mountains of the western United States, particularly that area centering on the Yellowstone National Park (Wyoming, Montana, and Idaho). The U.S. Rocky Mountains are considered the major center of diversity of *Antennaria*, but two other smaller centers exist in southeastern North America and the northwestern Arctic. Because the morphologically most primitive species occur in the major center of diversity, it is highly likely that the genus evolved in or near this area and radiated outward from there (BAYER and STEBBINS, 1987). A complete set of distribution maps for all the species discussed is presented in BAYER and STEBBINS (1987).

A well established relationship in *Antennaria* (BAYER and STEBBINS, 1987) as well as other agamic groups (GUSTAFSSON, 1947; BIERZYCHUDEK, 1985) is that the polyploid agamic complexes have wider geographic ranges than most of their sexual progenitors.

Additionally, the sexually reproducing species tend to be distributed in unglaciated regions, while the agamospecies occur primarily in previously glaciated areas (BAYER and STEBBINS, 1981, 1987). Cytogenetics has been very informative in studying the phytogeographic movements of certain taxa as well as discerning the area where specific polyploids may have arisen. For example, tetra-

ploid cytotypes of *A. neodioica* occur in the Appalachian region of the eastern United States, whereas higher cytotypes are distributed in all other areas of the range which stretches across North America between 40 and 60° north latitude (BAYER, 1985a; BAYER and STEBBINS, 1987). It is likely that the tetraploids arose in the Appalachians and that higher ploidy levels evolved and migrated to other areas since the end of the last glacial episode (BAYER, 1985a; BAYER and STEBBINS, 1987). Similarly, sexual tetraploid races of *A. parlinii* are infrequent and occur on the western margin of its range; the more widespread sexual and asexual hexaploids are the most common cytotype (BAYER, 1985b). Sexual diploid cytotypes of *A. media* occur in the Sierra Nevada and Inyo Mountains of California, whereas sexual and asexual tetraploids (infrequently higher ploidies) are much more widespread and abundant (BAYER and STEBBINS, 1987). *A. Friesiana* s.l., *A. marginata, A. monocephala, A. parvifolia,* and *A. umbrinella* each contain several cytotypes (BAYER and STEBBINS, 1987) and knowing the geographic distribution of these different cytotypes would be of great interest. In several agamic groups sexual populations of a species often occur at much lower elevations than agamospermous ones (BIERZYCHUDEK, 1985). However, there doesn't appear to be any significant correlation in *Antennaria* because sexual diploid populations of *A. aromatica* and *A. media* (BAYER, 1984) occur in alpine situations as high as asexual populations (BAYER, unpubl. obs.).

The distribution of sexual and agamospermous populations within each specific group is also noteworthy. In *Antennaria*, all diploid ($2n = 28$) populations, as far as we know, reproduce sexually and have a ± 50 % frequency of staminate clones in their populations (figure 2; The botanically correct terms staminate and pistillate are used to describe the sporophytes that produce either male or female gametophytes, respectively). Sexual populations have equal proportions of staminate and pistillate clones, as is revealed by gender ratio determinations. However, many of the polyploids reproduce via agamospermy (figure 2) and so populations are composed largely or entirely of pistillate clones (BAYER and STEBBINS, 1983).

Consequently, *Antennaria* is very useful as a tool to study the evolution of agamic complexes because sexual and asexual populations are easily discerned.

Antennaria parlinii, which is distributed throughout eastern North America, has both sexual and asexual populations (BAYER and STEBBINS, 1983; MICHAELS and BAZZAZ, 1986). A detailed study in Ohio and neighboring West Virginia revealed that sexual populations (as indicated by gender ratios) were found primarily in the unglaciated regions of these states, where suitable habitats for colonization are diverse, numerous and close together. Asexual populations were confined entirely to the glaciated parts of Ohio where suitable habitats are few, far apart, and more similar to each other with respect to edaphic conditions (BAYER and STEBBINS, 1983). Sexual populations occur in the unglaciated region where safe sites for colonization are close together, yet heterogeneous, whereas the asexual populations are found in the glaciated terrain where safe sites are far apart yet homogeneous (BAYER and STEBBINS, 1983). At the glacial margin, several populations were discovered that had "female-biased" gender ratios. These populations contained a mixture of sexuals, asexuals, and probable facultative sexuals (BAYER and STEBBINS, 1983). "Facultative" clones kept in isolation produced asexual achenes in the center whorls of the capitulum, whereas the outer achenes, presumably with sexual embryo sacs, remained undeveloped.

MICHAELS and BAZZAZ (1986) have presented some evidence for differences in colonizing and competitive ability between sexual and asexual *A. parlinii.* Asexual plants produce a larger number of seeds of lighter mass than sexuals. However, because the survivorship of sexual seedlings is greater, the recruitment of sexual and asexual progeny was not significantly different (MICHAELS and BAZZAZ, 1986). The major advantage of the asexual seeds over sexual ones appears to be in their greater potential for dispersibility. Stolon production can be used as a measure of competition and stolons of asexuals had the highest mortality, whereas staminate sexual clones had the lowest. Vegetative reproduction in sexuals is characterized by long-lived and wandering stolons that perhaps enhance competitive ability in an unpredictable environment (MICHAELS and BAZZAZ, 1986). Sexuals probably have an advantage in the more competitive environment as the result of the higher adult survivorship. Additional demographic studies with *A. parlinii,* and other species that have both sexual and asexual populations, are necessary before meaningful general conclusions can be drawn concerning the colonizing and competitive ability of the two reproductive modes.

Additional species in which both sexual and asexual populations are known are *A. aromatica, A. frie-*

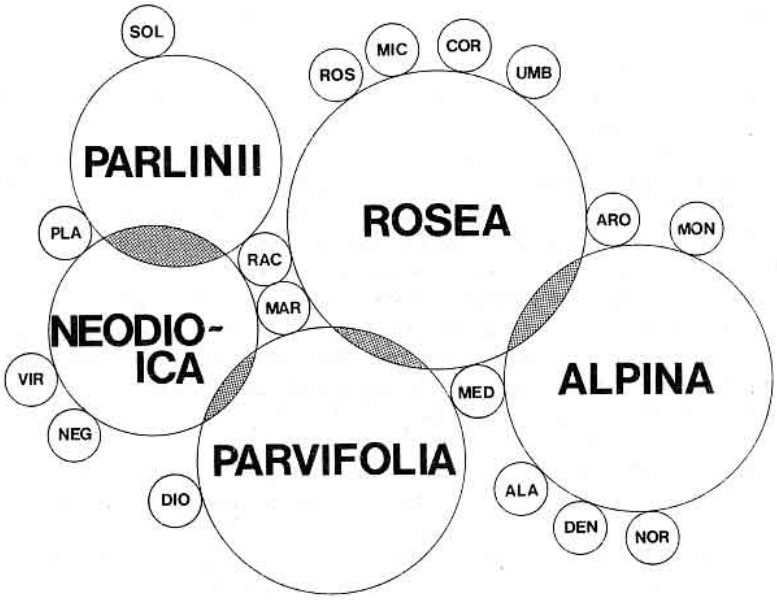

Fig. 1. Relationship of the five polyploid agamic complexes to each other and to sexual progenitors. Size of the taxonomic group is indicative of the relative amounts of morphological variation within each taxon. Shading indicates areas of morphological overlap between the polyploid complexes. Sexual progenitors are labeled with the first three letters of their specific or subspecific epithets: *A. aromatica* (ARO), *A. corymbosa* (COR), *A. densifolia* (DEN), *A. dioica* (DIO), *A. friesiana* subsp. *alaskana* (ALA), *A. marginata* (MAR), *A. media* (MED), *A. microphylla* (MIC), *A. monocephala* (MON), *A. neglecta* (NEG), *A nordhagiana* (NOR), *A plantaginifolia* (PLA), *A. racemosa* (RAC), *A. rosulata* (ROS), *A. solitaria* (SOL), *A. umbrinella* (UMB), and *A. virginica* (VIR). Contact between sexual progenitors and the polyploid complexes indicates possible contributions of genes from that sexual to the polyploid. Some sexuals (RAC, MAR, and MED) are pivotal genomes because they have probably contributed genes to more than one complex. See text for further explanations

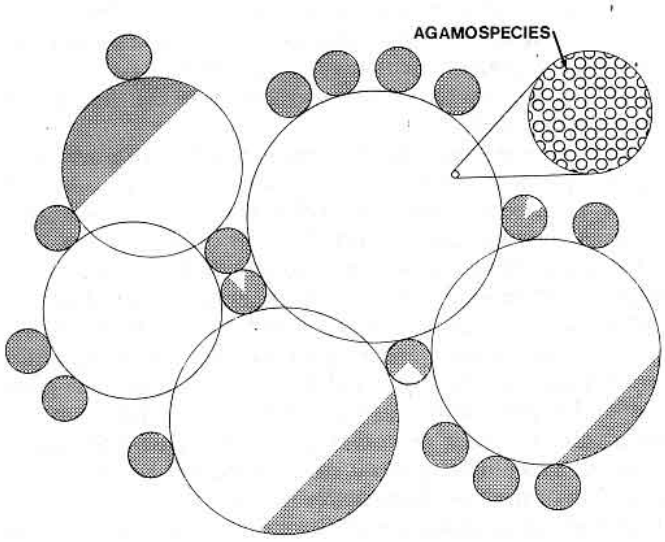

Fig. 2. Occurrence of amphimixis (sexual reproduction) and agamospermy (asexual seed production) in the *Antennaria* agamic complexes and related diploids. Shaded areas indicate the presence of amphimixis. White or nonshaded areas indicate the predominance of agamospermy. In groups where the sexual and asexual reproduction occur the relative proportions are speculative at this point. Each agamic complex is composed of innumerable agamospecies (microspecies), which have small amounts of morphological variation and are slightly discontinuous from one another morphologically. All the agamospecies considered together constitute the agamic complex. Taxa are the same as those given in figure 1

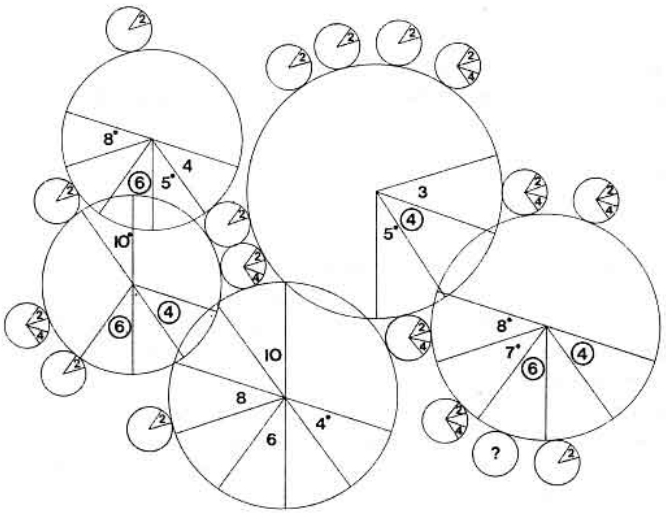

Fig. 3. Distribution of cytotypes within the *Antennaria* agamic complexes and related sexual species. Numbers within the pie diagrams indicate the cytotypes that have been reported for each species: 2 = diploid (2n = 28), 3 = triploid (2n = 42), 4 = tetraploid (2n = 56), etc. Circled numbers indicate the cytotype(s) that appear to be the most frequently occurring one(s) within a given complex. A star (*) next to a cytotype indicates that this count has been reported from only one or two collections. ? = the chromosome number of *A. densifolia* is unknown. Relative position of each cytotype within the "pie" is the same for each species so that direct comparisons regarding the distribution of cytotypes within and among species can be made. Taxa labels are the same as those given in figure 1

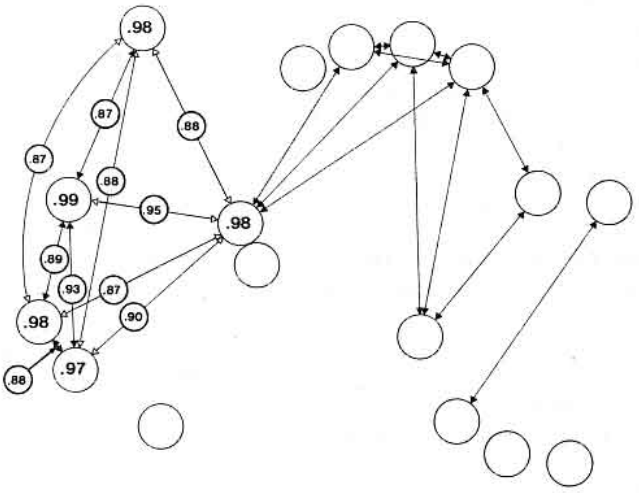

Fig. 4. Indicators of divergence and isolation among sexual *Antennaria* as indicated by hybridization and genetic identities among the species. Taxa are labeled as in figure 1. Solid headed arrows signify reported hybrids between certain taxa. Values within a given taxon (NEG, PLA, RAC, SOL, VIR) are average genetic identities from infraspecific comparisons of populations. Circled values on lines with hollow arrowheads are average genetic identities for interspecific comparisons between the taxa indicated. See text for further explanations

siana (Trautv) Ekman subsp. *friesiana* (= *A. alpina)*), *A. marginata, A. media, A. parlinii*, and *A. parvifolia*, but the distributions of the different reproductive modes in most are poorly known (figure 2). In *A. parvifolia*, sexual populations occur primarily in the southern portion of the range (southern Rockies), whereas asexual ones occur in the north (BAYER and STEBBINS, 1987). STEBBINS has determined that sexual races of alpine *A. media* occur primarily in California and Oregon, whereas asexual ones occur throughout the remainder of the range to the east and north (G. L. STEBBINS, unpubl obs.).

The processes by which new agamospermous clones are generated can only be speculated upon at this point. Possibly facultatively agamospermous clones, which produce some sexual embryo sacs yet evidently also possess genes necessary for the production of agamospermous ones, are primarily responsible.

Complexes, such as tetraploid *A. rosea*, are interesting because staminate clones are extremely rare,

the species being entirely agamospermous (figures 1 and 2). The question can be asked: How do new agamospermous clones arise in *A. rosea*? Perhaps occasional sexual embryo sacs are produced by these clones and these in turn are pollinated and subsequently fertilized by compatible pollen from sexual tetraploid relatives (figure 3). The occurrence and evolutionary importance of facultative agamospermy in *Antennaria* is yet to be determined.

Morphology, cytology, and genetics of the sexual species

All sexual species, that have been investigated (JUEL, 1900; STEBBINS, 1932a; URBANSKA, 1959, 1961) reproduce via the polygonum-type, 8-nucleate embryo sac common to most sexually reproducing angiosperms (figure 2). It is important to note that most agamic complexes have sexual members that are strong outcrossers (i. e. dioecious, monoecious, or self-incompatible). *Antennaria* follows this pattern, as the sexual taxa are dioecious.

Most of the sexuals have relatively narrow geographic ranges (BAYER and STEBBINS, 1987) and are well-defined morphologically (BAYER, 1985a). A few have very narrow ranges and somewhat strict edaphic requirements, e.g. *A. aromatica* is found on talus (usually limestone) in southwestern Montana (EVERT, 1984; BAYER and STEBBINS, 1987) and *A. virginica* occurs primarily on Devonian age shale barrens principally in West Virginia (STEBBINS, 1935; BAYER 1985a; BAYER and STEBBINS, 1987). These geographic ranges and edaphic requirements are narrow in comparison to that of the polyploid complexes. Other sexual species have extraordinarily large distributions, such as *A. neglecta* which occurs from the east coast of North America to the Northwest Territories (BAYER and STEBBINS, 1987) and *A. dioica*, which extends across Eurasia from the British Isles to the Aleutian Islands. The ranges of most of the sexuals are intermediate to these extremes. Most of the sexual taxa occur in regions that were unglaciated during the Wisconsin glacial period (BAYER and STEBBINS, 1987) and the range of each specific sexual is usually sympatric, or at least partially so, with that of its polyploid derivatives.

The diploids each appear to have specific habitat requirements. In Montana, where as many as five sexuals (*A. aromatica, A. corymbosa, A. microphylla, A. racemosa,* and *A. umbrinella*) can occur on the same mountain slope, it appears that each species has rather distinctive habitat requirements (BAYER, unpubl. obs.). Some hybrid habitats exist and this allows for parapatric or mixed populations to occur on mountain slopes and subsequent hybridization among the following species to take place; *A. aromatica* (subalpine/alpine on talus, usually limestone), *A. corymbosa* (subalpine/alpine, very mesic places), *A. microphylla* (steppe and lower montane, among sagebrush or along streams), *A. racemosa* (montane/subalpine in moister coniferous forests), and *A. umbrinella* (steppes to subalpine, drier areas among sagebrush or under Ponderosa pine; BAYER, unpubl. field notes).

It has been demonstrated that the sexual diploids are usually morphologically distinct from each other (BAYER, 1985a; BAYER, in press a) and that they have diverged with respect to both vegetative and reproductive morphological features. Divergence at genes specifying soluable enzymes is another measure of relationship that can be used to compare the sexual taxa. Enzyme electrophoresis was used to determine the degree of divergence among five sexual species; *A. neglecta, A. plantaginifolia, A. racemosa, A. solitaria,* and *A. virginica* (BAYER and CRAWFORD, 1986). The average genetic identities (I) within each diploid species are very close to 1.00 (figure 4); I = 0.97, 0.99, 0.98, 0.98, and 0.98 for *A. neglecta, A. plantaginifolia, A. racemosa, A. solitaria,* and *A. virginica*, respectively. This indicates that populations within each species are very similar to one another with respect to alleles present at a locus and frequency of those alleles. When interspecific comparisons are made the average genetic identities are somewhat lower (figure 4) indicating there has been some divergence among the species at the loci surveyed. Although the five taxa studied have diverged a great deal from one another with respect to morphology they haven't diverged nearly as much with respect to loci coding the 20 isozymes that were assayed (BAYER and CRAWFORD, 1986). The lack of concordance between morphological and biochemical divergence has been similarly noted for other plant groups (BAYER and CRAWFORD, 1986).

Enzyme electrophoresis has been useful in demonstrating the autopolyploid origin of tetraploids in several plant groups such as *Tolmiea menziesii* (Saxifragaceae; SOLTIS and RIESEBERG, 1986) and

Coreopsis grandiflora var. *longipes* (Asteraceae; CRAWFORD and SMITH, 1984) as well as *A. virginica* (BAYER and CRAWFORD, 1986). Diploid and tetraploid races of *A. virginica* have very high genetic identities when intercytotypic comparisons (I = 0.98) are made (BAYER and CRAWFORD, 1986). The high identity value supports the hypothesis (BAYER and STEBBINS, 1981, 1982; BAYER, 1984) that the tetraploid cytotypes of *A. virginica* are autopolyploid derivatives of the diploid. In addition, both cytotypes contain identical alleles at all loci, except that one population of tetraploid *A. virginica* contained a *Pgi-3* allelic variant at a low freqency of 0.17 (BAYER and CRAWFORD, 1986). The narrowly restricted edaphic endemic, *A. virginica*, (STEBBINS, 1935; BAYER and STEBBINS, 1982), has as a larger gene diversity value (HT = 0.107) than the two more geographically widespread and ecologically broad taxa *A. neglecta* (HT = 0.098) and *A. plantaginifolia* (HT = 0.066; BAYER and CRAWFORD, 1986).

Occurrence and evolutionary significance of hybridization

Hybridizations are a necessary step in the evolution of polyploid agamic complexes. Interspecific F1 hybrids are frequently found in communities where two or more sexual species occur sympatrically. Such hybrids are usually easy to identify because they are morphologically intermediate between their parents. However, later generation backcross progeny and introgressant segregates may be very difficult or impossible to distinguish morphologically from their recurrent parent. Later generation hybrids become polyploidized and acquire agamospermy becoming fully fertile agamic microspecies.

Many interspecific F1 hybrids between predominantly sexual diploid species have been identified since the first discovery of putative hybrids between *A. plantaginifolia* and *A. neglecta* (STEBBINS, 1932a; figure 4). URBANSKA (1968b, 1969) has recorded intersectional hybrids between *A. dioica* and *A. carpatica*. Recently, numerous putative interspecific hybrids have been reported: *A. friesiana* ssp. *alaskana* × *A. monocephala* (BAYER and STEBBINS, 1987); *A. aromatica* × *A. umbrinella* (CHINNAPPA, 1986); *A. corymbosa* × *A. media* (BAYER and STEBBINS, 1987), *A. corymbosa* × *A. microphylla* (BAYER and STEBBINS, 1987), *A. corymbosa* × *A. racemosa* (BAYER and STEBBINS, 1987); *A. media* × *A. umbrinella* (BAYER, 1984; CHINNAPPA, 1984); *A. microphylla* × *A. racemosa* (BAYER, in press b), *A. microphylla* × *A. umbrinella* (CHINNAPPA, 1984; BAYER and STEBBINS, 1987); *A. neglecta* × *A. virginica* (BAYER and STEBBINS, 1982); *A. plantaginifolia* × *A. solitaria* (BAYER, 1985a), *A. plantaginifolia* × *A. virginica* (BAYER and STEBBINS, 1982); *A. racemosa* × *A. umbrinella* (BAYER and STEBBINS, 1982, 1987; figure 4). In cases where the chromosome numbers of these species have been determined, they are almost always diploid (2n = 28) and only occasionally triploid (BAYER and STEBBINS, 1987).

The interspecific hybrids appear to occur in habitats that are intermediate to those in which their parents are usually found (BAYER and STEBBINS, unpubl. field notes, 1980, 1982, 1984; BAYER, unpubl. field notes, 1985, 1986). This is especially evident in the mountains of western North America, where the habitat types can shift abruptly over relatively short intervals.

Interspecific hybrids have been identified using several lines of evidence. They are morphologically intermediate between their putative parents and in several cases they have been compared via numerical taxonomic methods to artificially synthesized interspecific hybrids (BAYER, 1985a, b; BAYER, in press a). In one case a suspected hybrid between *A. corymbosa* (a diploid) and *A. media* (a tetraploid) was determined as triploid (BAYER and STEBBINS, 1987). Additionally, enzyme electrophoresis has been used in identifying hybrids because the parental species may have divergent alleles at several loci and the hybrids are heterozygous (BAYER and CRAWFORD, 1986).

Preliminary data suggest that the occurrence of hybridization could be quite frequent. Seeds were collected from a population of sexual diploid *A. corymbosa* (BAYER and LEBEDYK # *M-508*) which were growing along a subalpine stream in Montana. In the forest nearby (within 30 meters) was a population of sexual diploid *A. racemosa* (BAYER and LEBEDYK # *M-509*). The seeds of *A. corymbosa* were sown and transplanted at a very young stage, when all *Antennaria* look similar. Later it was observed that two plants among 55 (3.6%) looked very different. These plants were undoubtedly interspecific hybrids between *A. corymbosa* and *A. racemosa*, as was confirmed by enzyme electrophoresis and later by morphology when they flowered (BAYER, unpubl. obs.). It follows that

the formation of interspecific hybrids in nature could be relatively frequent under certain conditions.

Much of our knowledge of hybrids in *Antennaria* comes from artificially synthesized interspecific hybrids and backcross progeny. The fertility of artificial interspecific hybrids is usually rather low (BAYER and STEBBINS, 1982; BAYER, 1985a). Seed set as a result of interspecific hybridizations is usually low as well, but in some cases hybridization is more successful. e.g. hybrids between *A. neglecta* and *A. solitaria* produced average seed set of 84.0 %.

Additionally, the pollen stainability of the F1 hybrids was relatively lower, generally from 51.0 % to 80.0 %, whereas that of natural occurring diploids is ordinarily above 85.0 % (BAYER, 1985a). Cytogenetic analysis of artificial interspecific hybrids among several of the diploids (BAYER, 1984) has suggested that these sexual taxa differ by one or more inversions, as meiotic irregularities are observed in meiocytes of the hybrids.

The sexual diploid species of *Antennaria* seem to fit most closely into the *Geum* fertility relationship pattern (*sensu* GRANT, 1981). They are obligately outcrossing, perennial herbs in which floral isolating mechanisms are apparently poorly evolved. The pollinators of *Antennaria* include a variety of flies (Diptera; families Bombyliidae and Syrphidae) and bees (Hymenoptera: Apoidea; families Andrenidae and Halictidae) (H. MICHAELS pers. comm.; BAYER field observations). These pollinators are unfaithful and probably visit a wide variety of plant species.

Relatively wide interspecific crosses between species from different sections of the genus and from widely separated allopatric ranges (example: *A. racemosa* × *A. virginica*, BAYER, 1985a) are attainable, but are largely sterile. URBANSKA documented intersectional hybrids between *A. dioica*, a stoloniferous species, and *A. carpatica*, a non-stoloniferous species (URBANSKA 1968b, 1969). Several attempted crosses between other stoloniferous species (e.g. *A. plantaginifolia*) and members of the non-stoloniferous group (e.g. *A. lanata*) have been unsuccessful (BAYER, unpubl.), as have interspecific crosses between *Antennaria* and related genera such as *Gnaphalium* and *Anaphalis* DC.

Reproductive isolating mechanisms are poorly developed between species that have very different habitat requirements and therefore many species seem to be isolated primarily by environmental and spatial isolating mechanisms, but when these fail hybrids and introgressant segregates are frequently found (BAYER and STEBBINS, 1982).

Interspecific hybrids can often be used to determine the mode of inheritance of particular morphological characters. Most of the characters which have been studied (BAYER, 1985a, b) are inherited polygenically; the character state in the hybrid appearing intermediate between the parents. The hybrids are generally of intermediate morphology between their parents, however in some cases they may resemble one more than the other (BAYER, 1985a, b). Some B1s that have been generated [*(A. neglecta* × *A. racemosa)* × *A. neglecta*], look almost identical to the recurrent parent *(A. neglecta)*, demonstrating that a single generation of backcrossing can significantly change the morphology of the F1s (BAYER, 1985a). Consequently, introgressant segregates could be common in communities where interspecific hybridization is taking place. These would be undetectable based on morphology, but could possibly be revealed using biochemical genetics.

The evolutionary significance of the interspecific hybrids and hybrid segregates probably lies in the later generations that become polyploidized, acquire agamospermous seed production and evolve into microspecies (agamospecies). The mechanisms behind these metamorphoses are poorly understood and the genetic basis of agamospermy in *Antennaria* is unknown. The mode of inheritance of agamospermy will be difficult to ascertain because agamospermous pistillate plants produce no pollen to be used in experimental crosses. Similarly, sexual staminate and pistillate individuals carrying genes for agamospermy are difficult to detect. The one hope is that facultatively agamospermous individuals can be isolated, these plants are at least partially sexual yet carry genes for agamospermy and could used in experimental series of crosses.

Evolution of the polyploid agamic complexes

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 (figures 2 and 3). If the basis for this variation is determined, then the patterns of variation become comprehensible. The source of the morphological variation in the polyploids resides with their sexual diploid and tetraploid ancestors (figures 1–3). Consequently, the sexual species must first be delimited and studied before the variation within the polyploid agamic complexes can be explained and circumscribed.

Of the five agamic complexes (figure 1), only *A. neodioica* and *A. parlinii* are reasonably well known with respect to cytology, ecology, morphology, phylogenetic relationships, reproductive modes, and taxonomy (STEBBINS, 1932a, b; BAYER and STEBBINS 1981, 1982, 1983, 1987; BAYER, 1984, 1985a, b; BAYER and CRAWFORD, 1986; MICHAELS and BAZZAZ, 1986). *Antennaria alpina* and *A. rosea* are currently under investigation (BAYER, in press a, b; STEBBINS unpubl. obs.) and offer considerably greater challenge than the *A. neodioica* and *A. parlinii* complexes because the patterns of morphological variation are much more intricate. *Antennaria parvifolia* is poorly known, but has the interesting features of very high ploidy levels as well as having both sexual and asexually reproducing populations (BAYER and STEBBINS, 1987).

The geographic ranges of the agamic complexes are illustrated in BAYER and STEBBINS (1987), but will be discussed here briefly. *A. alpina* is basically circumboreal in its distribution, but the morphological variation is most complex in the North American Arctic and Canadian Rockies. *A. parvifolia* and *A. rosea* are distributed principally in the cordillera of Western North America, but *A. rosea* is also prevalent in the boreal forest region of Canada and west to Alaska. *Antennaria neodioica* and *A. parlinii* occur primarily in eastern North America, although some segregates of *A. neodioica* also occur in the forests of western North America. Considered as a single highly variable species, the polyploid segregates are much more widely distributed than are their diploid sexual progenitors (BAYER and STEBBINS, 1987).

The distribution of the different polyploid cytotypes (figure 3) within each complex is also of interest (a complete discussion of them can be found in BAYER and STEBBINS, 1987). Some complexes contain only a few cytotypes whereas others have a great diversity. *A. alpina* contains primarily hexaploid ($2n = 84$) cytotoypes (BAYER and STEBBINS, 1987), but these counts are primarily from Europe and it would be beneficial to have more determinations from North American material. When polyploid agamospermous members of the *A. media* complex are included within the *A. alpina* complex (figures 1 and 3) then, tetraploid, septaploid, and octoploid cytotypes must be added to those found in *A. alpina* sensu lato. *A. neodioica* has tetraploid ($2n = 56$), hexaploid, and decaploid ($2n = 140$) cytotypes (BAYER and STEBBINS, 1987), but the lower ploidy levels are apparently more prevalent (figure 3). Tetraploid, pentaploid, hexaploid, and octoploids are all known in *A. parlinii*, but the hexaploid cytotype is by far the most frequent (figure 3). Polyploidy in *A. rosea* (figure 3) has not evolved to very high levels as only triploids ($2n = 42$), tetraploids (most widespread and common) and pentaploids have been reported, whereas in *A. parvifolia* polyploidy is well evolved as tetraploids, hexaploids, octoploids, and decaploids have all been encountered and the higher ploidy levels appear to be most common (BAYER and STEBBINS, 1987). Although there is some morphological overlap among the *A. alpina, A. parvifolia*, and *A. rosea* complexes, they do have trends in ploidy level distribution that help delimit them. *A. rosea* is usually tetraploid (or at least has low ploidy such as triploid or pentaploid), *A. alpina* is usually hexaploid (*A. friesiana* ssp. *friesiana* is often tetraploid), and *A. parvifolia* has highest ploidy levels with octoploid and decaploid being more frequent and tetraploid and hexaploid less commonly encountered (figure 3).

The distribution of reproductive modes differs within each of the complexes and these can be used to distinguish them to some extent (figure 3). When *A. friesiana* subsp. *friesiana* and polyploid *A. media* are included within the *A. alpina* complex, then some sexual populations occur in this complex, but it is for the most part agamospermous. *Antennaria neodioica* and *A. rosea* are entirely agamospermous; staminate clones being very rare and when encountered are usually sterile (STEBBINS, 1932b; BAYER and STEBBINS, 1987). *A. parlinii* and *A. parvifolia* have both sexually and asexually reproducing populations (STEBBINS, 1932b; BAYER and STEBBINS, 1983, 1987) and the two types of populations appear to have different geographic distributions. Within *A. parlinii* the populations in the southwestern parts of the range are largely sexual, while those in the northern and eastern portions are predominantly agamospermous (BAYER and STEBBINS, 1983; BAYER, 1985b). Sexual populations of

A. parvifolia occur in the southern Rocky Mountains, whereas asexual ones are more prevalent in the northern parts of the Rockies (BAYER and STEBBINS, pers. obs.).

Various methodologies have been used to study the agamic complexes in *Antennaria*, including cytological (JUEL, 1900; STEBBINS 1932b; BAYER and STEBBINS, 1981; CHINNAPPA, 1984; BAYER, 1984; BAYER and STEBBINS 1987), morphological (BAYER, 1985a, b), crossability (BAYER and STEBBINS, 1982), ecological (BAYER and STEBBINS, 1983; MICHAELS and BAZZAZ, 1986), and enzyme electrophoretic techniques (BAYER and CRAWFORD, 1986). Cytological and fertility relationship studies are probably the most fundamental types of studies employed when first delimiting the sexual diploids and polyploids from one another.

Morphology and enzyme electrophoresis can be used to ascertain the extent to which the diploids and polyploids have diverged from one another and the existing amount of variation present.

The *A. parlinii* complex will serve as a case study of how these methods can be employed to unravel the evolutionary history of a polyploid agamic complex (figure 1). Initially, several diploids were chosen as possible diploid sexual progenitors of the *A. parlinii* complex (BAYER, 1985b), but the results of interspecific crossing experiments indicated that three diploids were the most likely candidates. *A. parlinii* has broad basal leaves with 3–7 primary veins, as do the diploids *A. plantaginifolia, A. racemosa*, and *A. solitaria*. When these diploids are crossed with diploids having only a single primary vein in their basal leaves (such as *A. neglecta* or *A. virginica*) the resultant interspecific hybrids have single-veined leaves (BAYER, 1985a). Therefore, the "small-leaved" *Antennaria* such as *A. neglecta* and *A. virginica* are unlikely ancestors of the *A. parlinii* complex. Additionally, many *A. parlinii* segregates have glabrous adaxial leaf surfaces and purple, stalked, glands on the flowering caulis and leaves (recognized taxonomically as *A. parlinii* ssp. *parlinii*) and these are characters found only in diploid *A. racemosa*.

The techniques of numerical taxonomy, such as principal components analysis (PCA), cluster analysis (UPGMA), discriminant analysis, and average similarity matrices were used to compare not only the three diploids and *A. parlinii*, but also the artificial interspecific hybrids. The artificial interspecific hybrids were used in the analyses with the thought that they would resemble morphologically some of the segregates of the *A. parlinii* complex. The results of these analyses are presented in BAYER (1985b), but the PCA from that paper has been redrawn and is presented here (figure 5). The *A. parlinii* complex is morphologically intermediate to the three diploids, indicating its probable hybrid origin from among these taxa (figure 5). The diploids form discreet morphological groups (especially if analyzed without the *A. parlinii* complex), which is typical of sexual diploid *Antennaria*. The morphological integrity of the diploids, notably *A. plantaginifolia*, is obscured by the presence of some *A. parlinii* segregates that morphologically resemble them. The artificial interspecific hybrids among the diploids are morphologically similar to many segregates of the *A. parlinii* complex, thus further indicating its probable hybrid origin from among these diploids.

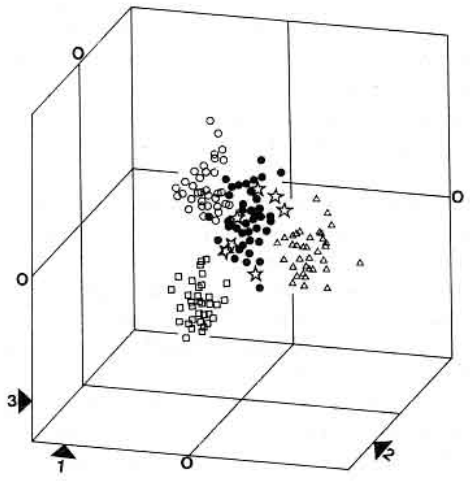

Fig. 5. PCA consisting of 149 operational taxonomic units (OTUs) including three diploid *Antennaria* species, artificially synthesized interspecific hybrids, and the polyploid *A. parlinii* s.l. (○) *A. plantaginifolia*, (□) *A. racemosa*, (△) *A. solitaria*, (●) *A. parlinii*, and (☆) interspecific hybrids.

Interspecific hybrid identifications are given as follows from uppermost to lowermost: *A. plantaginifolia* × *A. solitaria* (HY-03), *A. plantaginifolia* × *A. solitaria* (HY-01), *A. plantaginifolia* × *A. solitaria* (HY-02), *A. solitaria* × *A. racemosa* (HY-04), *A. racemosa* × *A. plantaginifolia* (HY-42), *A. racemosa* × *A. plantaginifolia* (HY-40), and *A. plantaginifolia* × *A. racemosa* (HY-43)

Enzyme electrophoretic analyses were used to test the hypothesis for the multiple hybrid origin of the polyploids formulated based on morphology (BAYER and CRAWFORD, 1986). Complete results of the studies of the enzyme electrophoresis of *A. parlinii* (and A. neodioica) can be found in BAYER and CRAWFORD (1986), but some of the results are summarized below.

Two loci, *Lap* (leucine amino peptidase) and *Pgi-3* (phosphoglucose isomerase) were very useful in documenting the origin of *A. parlinii*. Each of the diploids (*A. plantaginifolia, A. racemosa,* and *A. solitaria*) have unique alleles at these loci and these alleles can then be employed to verify the origin of the polyploids (BAYER and CRAWFORD, 1986). In *A. parlinii* s.l., the alleles present at *Lap* and *Pgi-3* are basically a composite of those found in the diploids *A. plantaginifolia, A. racemosa,* and *A. solitaria*. The analysis also points to the fact that some segregates of *A. parlinii* have alleles characteristic of one diploid, while others have two or sometimes three. This indicates that the complex is composed of individuals/populations with different combinations of the diploid genomes in their genetic composition (BAYER and CRAWFORD, 1986).

In many instances morphology and biochemical genetics are in direct concordance. Most of the *A. parlinii* segregates have alleles at *Lap* and *Pgi-3* that are the same as those found in *A. plantaginifolia*. One population of *A. parlinii* from West Virginia had capitulescences composed of 1, 2 or 3 heads (the usual situation in *A. parlinii* is 8–10 heads), suggesting that the genome of monocephalous *A. solitaria* was present in these polyploids. Electrophoresis confirmed the presence of the diagnostic alleles of both *A. plantaginifolia* and *A. solitaria*. Additionally, many glabrous-leaved *A. parlinii* segregates had alleles unique to glabrous-leaved *A. racemosa* (BAYER and CRAWFORD, 1986).

All of the analyses support the relationship of the polyploid *A. parlinii* to the diploids *A. plantaginifolia, A. racemosa,* and *A. solitaria*. From a genetic and morphological point of view, *A. parlinii* can be described as those segregates that are primarily hexaploid, contain genes from *A. plantaginifolia, A. racemosa,* and *A. solitaria*, and have morphological characteristics that can be attributed to one or more of the three diploids (figure 1).

Similar analyses with the *A. neodioica* complex (BAYER, 1985a; BAYER and CRAWFORD, 1986) have demonstrated that this complex should be thought of as those polyploids that have various combinations of genomes from *A. neglecta, A. plantaginifolia, A. racemosa,* and *A. virginica* (figure 1). Morphology and enzyme electrophoresis indicate that most of the segregates have genes from *A. neglecta* and *A. virginica* and that *A. plantaginifolia* and *A. racemosa* are less prevalent (BAYER, 1985a; BAYER and CRAWFORD, 1986). Additionally, *A. marginata* may be involved somewhat in the genetic composition of those *A. neodioica* isolates that lie in the morphological "gray area" where the *A. neodioica* complex (figure 1) melds into the *A. parvifolia* complex (BAYER, pers. obs.).

Antennaria rosea is currently under investigation (BAYER, in press a, b), but more research is needed before relationships can be firmly established. It appears, based on morphology and preliminary electrophoretic data, that the *A. rosea* complex is the result of hybridization among eight diploids, namely *A. aromatica, A. corymbosa, A. marginata, A. media, A. microphylla, A. racemosa,* and *A. umbrinella* (BAYER, unpubl. obs.). As a result of its diverse parentage, *A. rosea* is more perplexing and intricate than the *A. parlinii* or *A. neodioica* complexes (figure 1). Preliminary morphological observations indicate that *A. parvifolia* is related to sexual forms of *A. dioica, A. marginata,* and *A. media*, whereas *A. alpina* is the result of hybridization among the diploids *A. aromatica, A. densifolia, A. friesiana* ssp. *alaskana, A. media, A. monocephala,* and *A. nordhagiana* (BAYER, pers. obs.; figure 1).

The fact that some segregates of the *A. parlinii* complex resemble those of *A. neodioica* (BAYER, 1985b; BEALS, 1968) is the result of the sharing of the *A. plantaginifolia* and A. racemosa diploid genomes (figure 1). Pivotal genomes could be responsible for the morphological continuum that exists among the five agamic complexes. *A. aromatica, A. marginata, A. media, A. plantaginifolia,* and *A. racemosa* are apparently the pivotal genomes because they could be responsible for *A. parlinii* overlapping morphologically with *A. neodioica*; *A. neodioica* in turn with *A. parvifolia*; *A. parvifolia* subsequently with *A. rosea*; and *A. rosea* with *A. alpina* (figure 1). The entire polyploid agamic complex in the genus *Antennaria* could be one huge morphological cline, that can be conveniently separated into five relatively smaller and distinct polyploid complexes; *A. alpina, A. neodioica, A. parlinii, A. parvifolia,* and *A. rosea* (figure 1). The polyploid agamic complexes are natural units defined in genetic and morphological terms by the different sexual taxa that comprise their genetic composition (figure 1).

Methods of classification

Past practice has been to recognize each agamospecies as a distinct taxonomic entity, usually at the species rank. This has led to unwieldy classifications that can only be utilized by experts on the group. Clearly this method is unsatisfactory and a more reasonable scheme for classifying polyploid agamic complexes is one advocated by BABCOCK and STEBBINS (1938) in their classic evolutionary study of *Crepis* (Asteraceae). BAYER and STEBBINS (1982) used this method when revising the *A. parlinii* and *A. neodioica* complexes of the eastern United States.

Because the sexual diploids are morphologically discreet units they are each recognized as being distinct taxa at the rank of species. Polyploids that are morphologically identical with the sexual diploids (nonhybrid- or auto- polyploids), whether they are agamospermous or amphimictic, must be included as part of the sexual diploid. Consequently, tetraploid cytotypes of *A. virginica* and several other taxa are treated as synonymous with the sexual diploids because they are morphologically (BAYER and STEBBINS, 1982; BAYER, in press a) and, in the case of *A. virginica*, genetically (BAYER and CRAWFORD, 1986) inseparable from the sexual diploids. The remaining sexual and asexual polyploids that are of hybrid origin (segmental and genomic allopolyploids) are recognized at their own specific rank because their genetic composition is not attributable to any single diploid. Therefore, BAYER and STEBBINS (1982) classify *A. parlinii* as a distinct taxon from its sexual diploid progenitors, *A. plantaginifolia, A. racemosa*, and *A. solitaria*.

CRONQUIST (1945) recognized *A. parlinii* (sensu BAYER and STEBBINS, 1982) as two varieties of *A. plantaginifolia*, a view I oppose because the polyploids, while containing genes from *A. plantaginifolia* in their genetic background, also have portions of genomes from *A. racemosa* and *A. solitaria* (BAYER 1985b, BAYER and CRAWFORD, 1986). The polyploid complexes are each defined primarily by looking at their genetic composition as expressed phenotypically in their morphology as well as by enzyme phenotypes.

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