

## research reports

NICHE DIFFERENTIATION AMONG EIGHT SEXUAL SPECIES OF *ANTENNARIA* GAERTNER (ASTERACEAE: INULEAE) AND *A. ROSEA*, THEIR ALLOPOLYPLOID DERIVATIVE

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**Abstract**

*Antennaria rosea* is a hybrid polyploid complex that is widespread throughout western North America. The sexual progenitors of *A. rosea* include *A. aromatica*, *A. corymbosa*, *A. marginata*, *A. media*, *A. microphylla*, *A. racemosa*, *A. rosulata*, and *A. umbrinella*. The primary objective of this study was to investigate and quantify the habitat diversity in *A. rosea* and its sexual progenitors in order to determine whether the individual taxa are ecologically distinct. Ordination of species and environmental variables from the 101 study sites was carried out using Canonical Community Ordination (CANOCO). Results indicate that each sexual species of *Antennaria* appears to occupy a distinct niche. Both biotic factors, the community associates, and abiotic factors, the environmental variables, could be used to predict which species will occur in a given habitat and vice-versa. Many *A. rosea* populations did not occupy distinct niches themselves, but instead occupied niches that are very similar to those of their sexual progenitors. Some *A. rosea* populations occurred on sites which fell in between the groups of sites of the sexual species and these could be described as hybrid habitats. None of the *A. rosea* sites cover the range of abiotic conditions in which the sexual taxa occur. *Antennaria rosea* seems

to fulfil the prediction that in established floras polyploidy contributes intermediate 'fill-in' taxa that contribute to a more intensive partitioning of niche space. Polyploidy eventually leads to a saturation of most available niches by the progenitor taxa and their polyploid derivatives. This may be the most adaptively significant role that polyploids perform.

**Introduction**

*Antennaria* Gaertn. (Asteraceae: Inuleae) is a genus of dioecious perennial herbs that is widely distributed in temperate to arctic regions of the northern hemisphere. *Antennaria rosea* Greene is a morphologically diverse, hybrid polyploid complex that is common and widespread throughout western North America. The species is a gametophytic apomict and because the sexual species of *Antennaria* are dioecious, apomictic races have the same genetic constitution as their mothers and are gynoeious, composed entirely of pistillate plants. Morphometric and isozymic studies have demonstrated that *A. rosea* is the result of multiple hybridization from among as many as eight sexual species of *Antennaria* from western North America. These sexual species include *A. aromatica* Evert, *A. corymbosa* Nelson, *A. marginata* Greene, *A. media* Greene, *A. microphylla* Rydb., *A. racemosa* Hook., *A. rosulata* Rydb., and *A. umbrinella* Rydb. (Bayer, 1989c, 1990a). Taxa having both diploid and polyploid cytotypes are *A. aromatica*, *A. marginata*, *A. media*, and *A. umbrinella*, whereas *A. corymbosa*, *A. microphylla*, *A. racemosa*, and *A. rosulata* are sexually reproducing diploids (Bayer and Stebbins, 1987).

Based on informal field observations, each of the eight sexual species 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, 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 (Bayer, 1987a,

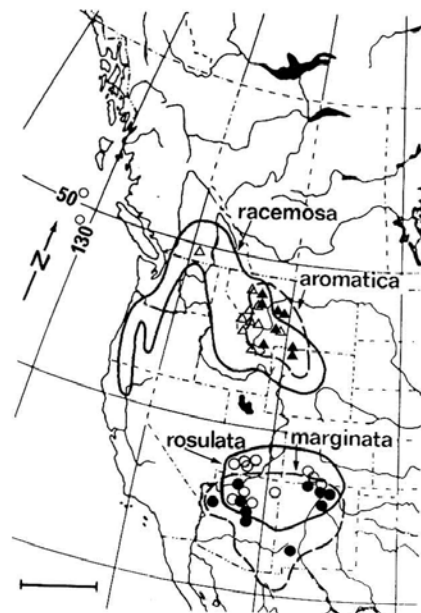
1990a). The montane zone in the understory of moist coniferous forests is the typical habitat of *A. racemosa* (Bayer, 1987a, 1990a). Both *A. aromatica* and *A. corymbosa* occur at timberline and marginally in the alpine zone, but the former is associated with limestone talus, while the latter is found in moist *Salix* thickets (Bayer, 1987a, 1989d). *Antennaria media* is found on dry, alpine tundra (Bayer, 1990c; Bayer *et al.*, 1990). In the southern Rockies, *Antennaria marginata* and *A. rosulata* also appear to occupy distinct habitats (Bayer, personal observations). Sexual populations appear to be isolated by ecological mechanisms only and as a result when two species grow in close proximity hybrids often occur (Bayer, 1987a).

*Antennaria rosea* occupies a wide variety of habitats from dry steppe to alpine tundra (Bayer, 1990a). It is often found sympatric with or in parapatric populations near its sexual relatives. 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). Casual field observations indicate that clones of *A. rosea* often resemble the sexual species that occur in habitats that are most similar to their own. It is likely that the ecological amplitude of *A. rosea* has 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. It is not clear whether *A. rosea* occupies only niches that are very similar to those of its sexual progenitors or whether it sometimes occurs in hybrid, intermediate or unique habitats.

As a part of a community, a plant population occupies part of 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' niche. One purpose of this study was to investigate and quantify the habitat diversity in *A. rosea* and its sexual progenitors to determine whether the individual taxa are ecologically distinct. An additional objective was to determine the potential value of environmental parameters and community associates as predictors of the various niches. 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 this study endeavours to contribute to our knowledge on that subject.

#### Materials and methods

Study sites were identified from herbarium specimens prior to the commencement of field work. Sites were chosen for each of the *Antennaria* species to represent the geographic range within which those species were known to occur. Voucher specimens of the *Antennaria*



**Fig. 1.** Ranges of *Antennaria aromatica*, *A. marginata*, *A. racemosa*, and *A. rosulata* and positions of 39 populations of the four species in relation to their ranges. Individual populations are labelled as follows: open circles = *A. rosulata*, closed circles = *A. marginata*, open triangles = *A. racemosa*, and closed triangles = *A. aromatica*. Bar = 500 km.

represented at each study site are deposited at ALTA. Figures 1–4 show the geographic localities of the 101 study sites as well as the margins of the ranges for each species and Table 1 lists the locality data. The number of study sites examined for each species was: *Antennaria aromatica* (8), *A. corymbosa* (10), *A. marginata* (10), *A. media* (10), *A. microphylla* (8), *A. racemosa* (10), *A. rosea* (24), *A. rosulata* (11), and *A. umbrinella* (10), for a total of 101 sites.

#### Environmental data

At each study site geographic (latitude and longitude) and climatic (mean annual temperature and precipitation (cm) from nearest weather station) values were recorded. Elevation above sea level (metres) and slope (degrees) were measured using a calibrated barometer and clinometer respectively. Aspect was measured and

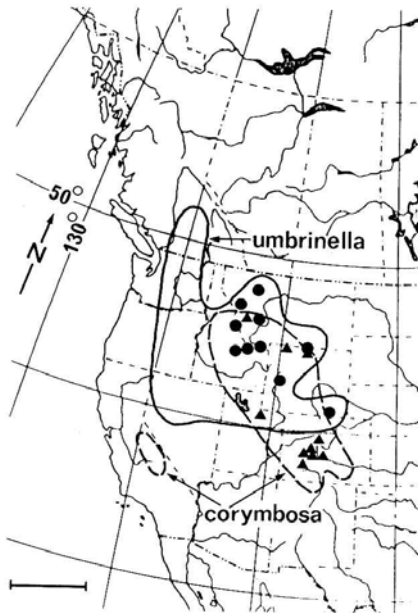


Fig. 2. Ranges of *Antennaria corymbosa* and *A. umbrinella* and positions of 20 populations of the two species in relation to their ranges. Individual populations are labelled as follows: closed circles = *A. umbrinella* and closed triangles = *A. corymbosa*. Bar = 500 km.

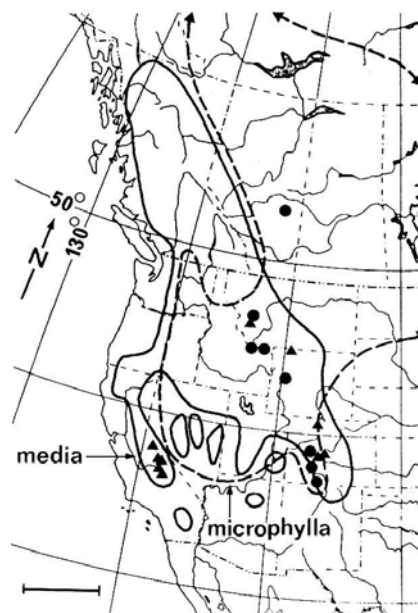


Fig. 3. Ranges of *Antennaria microphylla* and *A. media* and positions of 18 populations of the two species in relation to their ranges. The entire range of *A. microphylla* is not illustrated, but extends east to Minnesota and Hudson Bay and north to the southern Northwest Territories and northeastern British Columbia. Individual populations are labelled as follows: closed circles = *A. microphylla* and closed triangles = *A. media*. Bar = 500 km.

expressed in transformed azimuth degrees employing the procedure of Beers *et al.* (1966).

Shade, expressed as a relative measure provided by overhead canopy cover, was assessed by measuring the difference in light intensity between the study site and the adjacent open areas using a photometer equipped with a light quantum sensor. Soil temperature difference ( $^{\circ}\text{C}$ ) between the surface and 10 cm depth, and soil unconfined strength ( $\text{kg}/\text{cm}^2$ ), measured by a soil penetrometer, were recorded.

Soil samples were collected from each of the 101 study sites, allowed to air dry, and subjected to the following analyses. Soil water content (%  $\text{H}_2\text{O}$  on a dry mass basis) was determined by the gravimetric method of Gardner (1965), and soil organic matter (% weight loss on a dry mass basis) was determined by loss-on-ignition, employing the procedures of Ball (1964) and Broadbent (1965).

Soil texture was determined by the sedimentation

procedure of Day (1965). The pipette method of particle-size analysis (Day, 1965) was used to determine the relative proportions of the four size groups (gravel, sand, silt, clay) in each soil sample on a per cent dry mass basis.

Chemical analysis of soil samples from the study sites was performed by the High Volume Analysis Laboratory at the University of Alberta. The macronutrients measured include extractable forms of phosphorus ( $\text{PO}_4$ ), nitrogen ( $\text{NO}_3$ ,  $\text{NH}_4$ ), and sulphur ( $\text{SO}_4$ ), expressed in parts per million, as well as exchangeable forms of calcium (Ca), magnesium (Mg), and potassium (K), expressed in units of  $\text{mmol}/\text{kg}$ . The micronutrients include extractable manganese (Mn), iron (Fe), copper (Cu), and zinc (Zn) measured in parts per million, as well as exchangeable sodium (Na) measured in  $\text{nmol}/\text{kg}$ . Values were obtained by atomic absorption spectrophotometry.

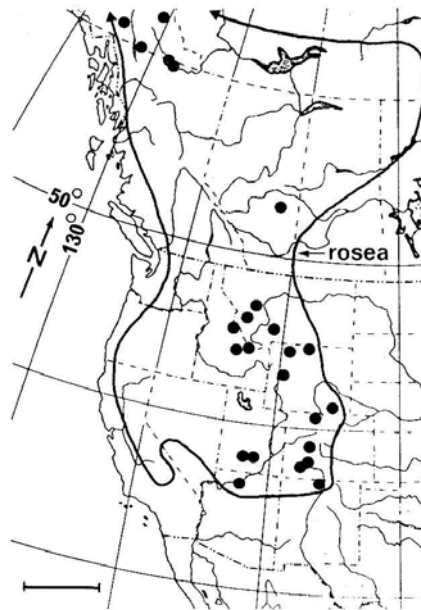


Fig. 4. Range of *Antennaria rosea* and positions of 24 populations in relation to the range. The entire range of *A. rosea* is not shown, but extends north to the Northwest Territories and Alaska and has disjunct populations on the north shore of Lake Superior, east and west shores of James Bay, and in Atlantic Canada. Individual populations are labelled as closed circles. Bar = 500 km.

metry or by using a Technicon Auto Analyzer. The per cent of carbonate on a dry mass basis was determined by titration.

#### Vegetative data

At each of the 101 study sites a 15 metre transect subdivided into three 5 metre intervals was sampled to determine the occurrence and abundance of all associated taxa. Species per cent cover was determined by application of the line-intercept method (Canfield, 1941) with the total per cent cover being the sum of the individual species cover estimates. Standard deviation of the total cover was calculated using values for the three different 5 metre intervals. Initial determinations of the associated vegetation were made using local floras while the final taxonomy follows Kartesz and Kartesz (1980). Associates were determined to the rank of species

whenever possible. However, due to the lack of flowering material at the time of collection, or to the taxonomic complexity of certain taxa, the genera *Aquilegia*, *Cirsium*, *Fragaria*, *Salix* and *Taraxacum* were determined only to the rank of genus and the taxa in the families Poaceae and Cyperaceae were combined into the general category 'Graminoids'. A total of 256 species were recorded from the 101 study sites.

#### Data analysis

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; Verwijst, 1988; John, 1989; Gignac and Vitt, 1990). This is the first study to use CCA for comparing adaptive syndromes of species and their hybrids. In this study, the ordination was performed to determine and visualize the habitat and species associates for the related *Antennaria* species and to see which environmental variables and species associates best distinguish the *Antennaria* species sites from one another.

The program was run with downweighting of rare species, and without any transformation of the variables, weighting environmental variables, or axis rescaling. One environmental variable (CLAY) was highly correlated with others and so was excluded from the analyses.

The data set was ordinated in two steps or analyses. Two CCA analyses were performed to separate the *Antennaria* species visually on the ordination diagram with respect to environmental variables. The first step separated three groups while the second step separated the remaining five groups. The polyploid *A. rosea* was included in both analyses, but did not separate as a group on any axis as did the eight diploid species. The Monte-Carlo permutation option of CANOCO was run to evaluate the significance of the ordination axes in both analyses.

The BMDP stepwise discriminant analysis (Dixon, 1981) was used to determine the *a posteriori* classification of samples into *a priori* defined classes of sites, namely the eight sexual taxa. Samples from *A. rosea* sites were not used in the calculation of the correlation matrix thus allowing their classification into one of the progenitor groups and determination of the similarity of the polyploid to the various diploid species based on environmental characters and associated species. A second discriminant analysis (DA) was performed for *a posteriori* classification of *A. rosea* into one of the *a priori* species groups, now including an *a priori* defined *A. rosea* group.

**Table 1.** Locality data for 101 populations of *Antennaria aromatica*, *A. corymbosa*, *A. marginata*, *A. media*, *A. microphylla*, *A. racemosa*, *A. rosea*, *A. rosulata*, and *A. umbrinella*, with species names, state/province, county, and collection numbers. Latitude, longitude and elevation (metres) above sea level are given parenthetically after each population designation. Voucher specimens are deposited at ALTA

*A. aromatica* Evert. U.S.A. Montana: Gallatin Co., *Bayer et al. MT-628* (45.9°, 110.9°, 2515); Madison Co., *Bayer et al. MT-634* (45.0°, 111.9°, 2899); Carbon Co., *Bayer et al. MT-642* (45.1°, 109.4°, 2972); Cascade Co. *Bayer et al. MT-747* (47.1°, 111.1°, 2136); Judith Basin Co., *Bayer et al. MT-754* (46.8°, 110.7°, 2432); Teton Co., *Bayer et al. MT-768* (47.9°, 112.7°, 2054); Lewis and Clark Co., *Bayer et al. MT-890* (47.4°, 112.7°, 2106). Wyoming: Park Co., *Bayer et al. WY-836* (44.7°, 109°, 2173).

*A. corymbosa* E. Nelson. U.S.A. Colorado: Gunnison Co., *Bayer et al. CO-810* (38.8°, 107.1°, 3048); *Bayer et al. CO-828* (39.1°, 107.1°, 3182); Hinsdale Co., *Bayer et al. CO-831* (38.0°, 107.2°, 3316); Gunnison Co., *Bayer et al. CO-863* (38.8°, 106.6°, 2896); *Bayer et al. CO-867* (38.8°, 106.4°, 3536); Summit Co., *Bayer et al. CO-877* (39.4°, 106.2°, 3127). Montana: Granite Co., *Bayer et al. MT-733* (46.2°, 113.2°, 1969). Utah: Summit Co., *Bayer et al. UT-617* (40.7°, 110.9°, 3194). Wyoming: Park Co., *Bayer et al. WY-711* (44.8°, 109.5°, 2899); Sheridan Co., *Bayer et al. WY-826* (44.8°, 107.8°, 2810).

*A. marginata* Greene. U.S.A. Arizona: Coconino Co., *Bayer et al. AZ-701* (34.9°, 111.4°, 2268); *Bayer et al. AZ-703* (34.4°, 111.3°, 2271); Mojave Co., *Bayer et al. AZ-705* (35.1°, 113.9°, 1939); Coconino Co., *Bayer et al. AZ-713* (35.2°, 111.6°, 2088); *Bayer et al. AZ-823* (36.4°, 112.1°, 2688). New Mexico: Sierra Co., *Bayer et al. NM-700* (32.9°, 107.8°, 2438); Santa Fe Co., *Bayer et al. NM-701* (35.7°, 105.8°, 2451); Taos Co., *Bayer et al. NM-704* (36.4°, 105.5°, 2353); Colfax Co., *Bayer et al. NM-800* (36.6°, 105.2°, 2396); Rio Arriba Co., *Bayer et al. NM-813* (36.9°, 107.0°, 2121).

*A. media* Greene. U.S.A. California: Inyo Co., *Bayer et al. CA-700* (36.5°, 118.2°, 3231); *Bayer et al. CA-707* (36.7°, 118.4°, 3225); Mono Co., *Bayer et al. CA-720* (37.9°, 119.3°, 3078); Inyo Co., *Bayer et al. CA-724* (37.2°, 118.6°, 3170); *Bayer et al. CA-732* (37.1°, 118.6°, 3237). Colorado: Gunnison Co., *Bayer et al. CO-849* (38.7°, 118.6°, 3719); Gunnison/Chaffee Co., *Bayer et al. CO-876* (38.8°, 106.4°, 3749); Routt Co., *Bayer et al. CO-883* (40.6°, 106.7°, 3152). Montana: Deerlodge Co., *Bayer et al. MT-722* (46.1°, 113.3°, 2774). Wyoming: Park Co., *Bayer et al. WY-705* (45.0°, 109.5°, 3200).

*A. microphylla* Rydb. Canada. Alberta: Beaver Co., *Bayer et al. AB-800* (53.1°, 115.6°, 671). U.S.A. Colorado: Conejos Co., *Bayer et al. CO-700* (37.1°, 106.4°, 2682); Saguache Co., *Bayer et al. CO-842* (38.2°, 106.9°, 2780); Gunnison Co., *Bayer et al. CO-864* (38.8°, 106.6°, 2896). Montana: Granite Co., *Bayer et al. MT-736* (46.2°, 113.3°, 1942); Beaverhead Co., *Bayer et al. MT-813* (44.6°, 111.6°, 2039); *Bayer et al. MT-814* (44.7°, 112.8°, 2027). Wyoming: Sublette Co., *Bayer et al. WY-600* (43.2°, 109.7°, 2298).

*A. racemosa* Hook. Canada. British Columbia: Yale Forest Reserve, *Bayer et al. BC-814* (49.8°, 119°, 1234). U.S.A. Montana: Gallatin Co., *Bayer et al. MT-707* (45.9°, 110.9°, 1865); Deerlodge Co., *Bayer et al. MT-713* (46.2°, 112.6°, 2147); Ravalli Co., *Bayer et al. MT-741* (46.2°, 113.8°, 1737); *Bayer et al. MT-800* (45.5°, 114.4°, 2042); Granite Co., *Bayer et al. MT-827* (46.5°, 113.8°, 1305); *Bayer et al. MT-831* (46.2°, 113.5°, 2018); Beaverhead Co., *Bayer et al. MT-866* (44.4°, 112.9°, 2469); Lewis and Clark Co., *Bayer et al. MT-883* (47.4°, 112.7°, 1640); Flathead Co., *Bayer et al. MT-895* (48.2°, 113.4°, 1987).

*A. rosea* Greene. Canada. Alberta: Beaver Co., *Bayer et al. AB-801* (53.1°, 115.6°, 701). British Columbia: Alaska Highway, *Lebedyk et al. BC-821* (59.7°, 127.3°, 671). Yukon: Smart River, *Lebedyk et al. YT-801* (60.0°, 131.7°, 884); Lake Laberge, *Lebedyk et al. YT-802* (61.0°, 135.1°, 762); Ross River, *Lebedyk et al. YU-803* (62.6°, 131.2°, 975); *Lebedyk et al. YU-805* (60.0°, 127.8°, 589). U.S.A. Arizona: Coconino Co., *Bayer et al. AZ-822* (36.4°, 112.1°, 2688). Colorado: San Juan Co., *Bayer et al. CO-800* (37.7°, 107.7°, 3203); Gunnison Co., *Bayer et al. CO-829* (39.1°, 107.1°, 3182); Hinsdale Co., *Bayer et al. CO-832* (38.0°, 107.2°, 3338); Routt Co., *Bayer et al. CO-884* (40.6°, 106.7°, 3152). Idaho: Custer Co., *Bayer et al. ID-602* (44.2°, 113.8°, 2535); Lemhi Co., *Bayer et al. ID-800* (45.5°, 114.3°, 2396). Montana: Gallatin Co., *Bayer et al. MT-701*; Granite Co., *Bayer et al. MT-737*; Lewis and Clark Co., *Bayer et al. MT-744*; Beaverhead Co., *Bayer et al. MT-857*. New Mexico: Rio Arriba Co., *Bayer et al. NK-811*. Utah: Garfield Co., *Bayer et al. UT-800*; Garfield Co., *Bayer et al. UT-822*. Wyoming: Sublette Co., *Bayer et al. WY-601*; Big Horn Co., *Bayer et al. WY-801*; Albany Co., *Bayer et al. WY-828*; Park Co., *Bayer et al. WY-837*.

*A. rosulata* Rydb. U.S.A. Arizona: Apache Co., *Bayer et al. AZ-800*; Coconino Co., *Bayer et al. AZ-700*; *Bayer et al. AZ-808*; *Bayer et al. AZ-817*. Colorado: Conejos Co., *Bayer et al. CO-701*; *Bayer et al. CO-702*. New Mexico: Rio Arriba Co., *Bayer et al. NM-707*. Utah: Garfield Co., *Bayer et al. UT-601*; *Bayer et al. UT-602*; *Bayer et al. UT-804*; *Bayer et al. UT-823*.

*A. umbrinella* Rydb. U.S.A. Idaho: Custer Co., *Bayer et al. ID-601*. Montana: Jefferson Co., *Bayer et al. MT-709*; Missoula Co., *Bayer et al. MT-743*; Teton Co., Lewis and Clark Co., *Bayer et al. MT-769*; Ravalli Co., *Bayer et al. MT-801*; Beaverhead Co., *Bayer et al. MT-809*; *Bayer et al. MT-854*. Wyoming: Sublette Co., *Bayer et al. WY-700*; Big Horn Co., *Bayer et al. WY-800*; Albany Co., *Bayer et al. WY-827*.

One-way analysis of variance was performed on the environmental variables using the ONEWAY procedure of SPSS-PC (Norusis, 1988) to calculate which variables were significantly different among species. Means and standard errors for the variables were calculated at the same time for each species.

### Results

Table 2 gives means and standard errors for all the environmental factors for each group of sites. Complete lists of relative abundance of community associates, as well as environmental data for each site are available from the senior author. The results of the CCA are presented as Fig. 5 (A–D), Fig. 6 (A–D), and Fig. 7 (A–D). Each site symbol rests at the centroid of the community associate species that occur at that given site. Therefore one can deduce which associate species are likely to be present at a given site based on its position on the graph. Because of the large and diverse species associates data set (256 species), visualization of the correspondence of specific associates and the *Antennaria* species was impractical and is not presented on these figures, but has been evaluated and will be discussed below.

In the ordination diagrams (Figs 5, 6 and 7), the lines representing environmental variables point in the direction of maximum change in that variable and the length of the line indicates a relative measure of the rate of the change in that variable (ter Braak, 1987). Therefore, longer lines are more important parameters than short ones and tend to be more closely related to the patterns of community variation (ter Braak, 1987). The relative position of each *Antennaria* species site can best be viewed by projecting the points onto the lines. This is accomplished by first extending each line, either on paper or in the mind, in both directions to the edge of the diagram. Then draw or visualize a line from the site symbols, perpendicular to the line until it intersects the line. The ranking of those endpoints along the line is an approximate indication of the relative value of the weighted average of each species site with respect to that environmental variable. Also, the origin of the line indicates the grand mean, therefore if the endpoint of the line lies on the same side of the origin as the perpendicular intersect then that site has a weighted average that is higher than the grand average and vice-versa in the other direction (ter Braak, 1986). For example, from Fig. 5 we can deduce that *A. racemosa* and *A. marginata* have the highest weighted means with respect to shade (i.e. they occur on the shadiest sites), *A. corymbosa*, *A. media*, *A. microphylla*, *A. rosea*, *A. rosulata*, and *A. umbrinella* have moderate means near the grand mean for all the sites (i.e. they occur on somewhat open sites), while *A. aromatica* sites have the lowest means (i.e. they almost always occur in full sun). The inclusion of *A. rosea* on

the ordination diagrams obscures the distinctness of the sexual taxa site groups. The *A. rosea* sites were not included in Figs 5 and 6, which are meant to illustrate the sexual species sites. Figure 7 shows the graphs of axis 1 vs 2 and 1 vs 3 of both CAA analyses (i.e. the same analyses as Figs 5 and 6), but these figures show only the sites for *A. rosea* and only the outlines of the distribution of sexual species sites. In this way the interrelations among all sites and groups can be seen by comparing Figs 5–7, without obscuring any of the relationships.

Figures 5, 7a, and 7c illustrate the results of the first CCA in which all taxa were included. The per cent variance accounted for in the first three axes in the graphs are 11.2, 10.0, and 9.3, respectively. The Monte-Carlo permutation option of CANOCO showed that the ordination was significant at the 5% level. Three taxa are most distinct in this analysis, namely *A. aromatica*, *A. marginata*, and *A. racemosa*. *Antennaria aromatica* sites form a well-defined group characterized by gravelly, non-silty, non-sandy soils with high amounts of calcium carbonate ( $\text{CaCO}_3$ ), sulphur (S), and low manganese (Mn). They are found at high elevations in full sun (Fig. 5). Two of the sites are close to *A. rosea* sites (Fig. 7A). Common community associates of *A. aromatica* include *Pinus flexilis*, *Draba oligosperma*, *Eritrichium nanum*, *Ivesia gordonii*, *Paronychia sessiflora*, and *Zygadenus elegans*. *Antennaria racemosa* occurs in habitats similar to those of *A. marginata*, but the two are widely separated latitudinally, *A. marginata* in the southern Rockies and *A. racemosa* in the northern Rockies (Fig. 1). The localities containing *A. marginata* or *A. racemosa* are usually on shady slopes with soil that is high in manganese. *Antennaria marginata* sites differ from *A. racemosa* ones in that they are more sandy, less sloped and have lower amounts of  $\text{PO}_4$  than *A. racemosa* sites (Table 1; Fig. 5). Also, *A. marginata* occurs at higher elevations than *A. racemosa* (Fig. 5). A coarse measure of patchiness, the standard deviation of cover among the three, 5 metre subtransects at a site (CSDEV), indicates that the *A. marginata* sites may be more patchy than *A. racemosa* ones. Most *A. racemosa* sites contained *Pseudotsuga menziesii*, *Spiraea betulifolia*, and *Xerophyllum tenax*, as community associates, whereas *A. marginata* localities commonly included *Pinus ponderosa*, *Lathyrus arizonicus*, *Pseudocymopterus montanus*, *Pteridium aquilinum*, *Quercus gambelii* and *Valeriana capitata*. Two populations of *A. marginata* are included within the *A. rosea* niche space (Fig. 7).

In order to facilitate the definition of the niches of the remaining taxa, the three species sites which were most divergent in the first analysis (i.e. *A. aromatica*, *A. marginata*, and *A. racemosa*), were removed and a second CCA performed. Figure 6, 7b and 7d display the

**Table 2.** Environmental data for nine species of *Antennaria* including *A. aromatica* (AROM), *A. corymbosa* (CORY), *A. marginata* (MARG), *A. media* (MEDI), *A. microphylla* (MICR), *A. racemosa* (RACE), *A. rosea* (ROSE), *A. rosulata* (ROSU), and *A. umbrinella* (UMBR). Presented are mean values ( $\pm$  s.e.) for 33 variables for the individual species sites and a mean value (MEAN) for all 101 sites. Variables include latitude (LATIT), longitude (LONG), elevation (ELEV), precipitation in cm (PREC), slope (SLOPE), mean air temperature (TEMP), aspect (ASPEC), shade (SHADE), soil temperature (SLTMP), soil moisture (SLWAT), soil unconfined strength (UNSTR), soil organic matter (ORG), % gravel in soil (GRAV), % sand in soil (SAND), % silt in soil (SILT), % clay in soil (CLAY), % cover (COVER), standard deviation of cover among the three subtransects (CSDEV), number of taxa in transect (NTAXA), and various soil nutrients ( $\text{CaCO}_3$ ,  $\text{NO}_3$ ,  $\text{NH}_4$ ,  $\text{PO}_4$ ,  $\text{SO}_4$ , Ca, Cu, Fe, K, Mg, Mn, Na, S, and Zn). Consult the text for details on the variables.

	AROM	CORY	MARG	MEDI	MICR
LATIT	46.2 $\pm$ 0.4	40.9 $\pm$ 1.0	35.5 $\pm$ 0.4	39.5 $\pm$ 1.1	43.2 $\pm$ 5.2
LONG	111 $\pm$ 1	108 $\pm$ 1	109 $\pm$ 1	113 $\pm$ 2	110 $\pm$ 2
ELEV	2410 $\pm$ 130	3000 $\pm$ 130	2300 $\pm$ 70	3250 $\pm$ 90	2170 $\pm$ 250
PREC	40.4 $\pm$ 2.8	44.2 $\pm$ 4.6	37.0 $\pm$ 3.6	37.4 $\pm$ 8.3	43.0 $\pm$ 4.5
SLOPE	16.0 $\pm$ 3.0	5.4 $\pm$ 2.1	32.1 $\pm$ 7.9	27.2 $\pm$ 5.1	0.6 $\pm$ 0.4
TEMP	5.1 $\pm$ 0.5	3.9 $\pm$ 0.8	11.0 $\pm$ 1.2	10.0 $\pm$ 1.5	4.1 $\pm$ 0.8
ASPEC	1.2 $\pm$ 0.2	1.7 $\pm$ 0.1	0.4 $\pm$ 0.2	0.5 $\pm$ 0.2	1.8 $\pm$ 0.2
SHADE	0.0 $\pm$ 0.0	10.0 $\pm$ 6.7	1530 $\pm$ 100	30.0 $\pm$ 30.0	0.0 $\pm$ 0.0
SLTMP	9.0 $\pm$ 1.8	7.8 $\pm$ 1.4	3.8 $\pm$ 0.8	7.6 $\pm$ 1.5	10.4 $\pm$ 1.69
SLWAT	12.8 $\pm$ 3.0	156 $\pm$ 106	10.5 $\pm$ 1.5	126 $\pm$ 110	23.5 $\pm$ 3.3
UNSTR	2.3 $\pm$ 0.4	1.4 $\pm$ 0.1	2.2 $\pm$ 0.4	2.5 $\pm$ 0.4	2.7 $\pm$ 0.5
ORG	5.0 $\pm$ 1.0	15.6 $\pm$ 1.8	6.5 $\pm$ 1.0	10.1 $\pm$ 2.5	9.5 $\pm$ 1.6
GRAV	50.4 $\pm$ 3.9	11.9 $\pm$ 3.6	18.5 $\pm$ 4.0	22.5 $\pm$ 4.0	10.2 $\pm$ 3.5
SAND	15.1 $\pm$ 6.2	34.1 $\pm$ 3.4	47.8 $\pm$ 4.2	46.1 $\pm$ 3.2	46.6 $\pm$ 5.3
SILT	30.9 $\pm$ 5.1	49.7 $\pm$ 4.0	30.8 $\pm$ 3.7	30.2 $\pm$ 4.4	39.0 $\pm$ 6.2
CLAY	3.6 $\pm$ 0.6	4.3 $\pm$ 0.6	2.9 $\pm$ 0.7	1.2 $\pm$ 0.3	4.2 $\pm$ 1.9
COVER	36.6 $\pm$ 5.6	91.0 $\pm$ 3.4	59.9 $\pm$ 7.6	64.4 $\pm$ 7.9	89.7 $\pm$ 5.0
CSDEV	8.6 $\pm$ 1.4	6.5 $\pm$ 2.7	12.9 $\pm$ 2.4	7.6 $\pm$ 2.2	3.7 $\pm$ 1.5
NTAXA	8.2 $\pm$ 0.7	10.6 $\pm$ 0.6	7.5 $\pm$ 0.8	6.2 $\pm$ 0.9	8.4 $\pm$ 0.7
$\text{CaCO}_3$	37.9 $\pm$ 8.8	0.9 $\pm$ 0.1	0.1 $\pm$ 0.0	0.1 $\pm$ 0.0	5.9 $\pm$ 3.9
$\text{NO}_3$	3.7 $\pm$ 1.4	5.6 $\pm$ 2.1	0.9 $\pm$ 0.1	1.7 $\pm$ 0.6	3.2 $\pm$ 1.5
$\text{NH}_4$	3.5 $\pm$ 0.7	12.0 $\pm$ 1.5	4.5 $\pm$ 0.6	6.3 $\pm$ 1.3	6.0 $\pm$ 1.0
$\text{PO}_4$	7.4 $\pm$ 2.7	5.7 $\pm$ 0.9	11.7 $\pm$ 3.4	8.3 $\pm$ 1.9	21.2 $\pm$ 8.6
$\text{SO}_4$	5.0 $\pm$ 0.8	9.2 $\pm$ 1.4	5.0 $\pm$ 0.9	5.6 $\pm$ 1.7	46.5 $\pm$ 16.5
Ca	354 $\pm$ 56	188 $\pm$ 36	124 $\pm$ 18	64 $\pm$ 25	463 $\pm$ 209
Cu	1.6 $\pm$ 0.3	4.5 $\pm$ 1.7	1.7 $\pm$ 0.5	1.2 $\pm$ 0.6	2.1 $\pm$ 0.4
Fe	29.1 $\pm$ 4.3	261 $\pm$ 32	61.4 $\pm$ 9.1	162 $\pm$ 81	39.5 $\pm$ 12.0
K	4.9 $\pm$ 0.7	4.7 $\pm$ 0.4	6.0 $\pm$ 0.9	3.9 $\pm$ 0.7	21.7 $\pm$ 7.6
Mg	24.2 $\pm$ 8.0	27.7 $\pm$ 7.8	26.0 $\pm$ 6.4	122 $\pm$ 116	453 $\pm$ 287
Mn	11.6 $\pm$ 2.9	18.4 $\pm$ 3.4	36.2 $\pm$ 6.9	22.6 $\pm$ 7.1	14.7 $\pm$ 2.2
Na	2.0 $\pm$ 0.8	2.7 $\pm$ 1.2	1.9 $\pm$ 0.5	1.6 $\pm$ 0.5	28.9 $\pm$ 17.3
S	7.6 $\pm$ 0.2	5.3 $\pm$ 0.2	5.9 $\pm$ 0.1	5.3 $\pm$ 0.2	7.8 $\pm$ 0.2
Zn	1.9 $\pm$ 0.6	3.0 $\pm$ 1.3	1.4 $\pm$ 0.3	1.5 $\pm$ 0.5	2.2 $\pm$ 0.8

	RACE	ROSE	ROSU	UMBR	MEAN
LATIT	46.6 $\pm$ 1.5	46.2 $\pm$ 8.6	36.9 $\pm$ 1.0	44.9 $\pm$ 1.9	42.6 $\pm$ 0.6
LONG	114 $\pm$ 1	114 $\pm$ 2	110 $\pm$ 1	111 $\pm$ 1	112 $\pm$ 1
ELEV	1840 $\pm$ 120	2150 $\pm$ 190	2660 $\pm$ 90	2090 $\pm$ 140	2400 $\pm$ 70
PREC	36.5 $\pm$ 2.0	37.3 $\pm$ 2.8	31.8 $\pm$ 3.3	32.7 $\pm$ 3.4	37.5 $\pm$ 1.4
SLOPE	19.7 $\pm$ 5.8	15.6 $\pm$ 2.8	24.3 $\pm$ 13.8	21.3 $\pm$ 13.9	18.1 $\pm$ 2.1
TEMP	6.5 $\pm$ 0.4	3.7 $\pm$ 0.9	8.0 $\pm$ 0.5	5.2 $\pm$ 0.5	6.1 $\pm$ 0.4
ASPEC	1.0 $\pm$ 0.3	1.4 $\pm$ 0.1	1.4 $\pm$ 0.2	1.3 $\pm$ 0.2	1.2 $\pm$ 0.1
SHADE	1510 $\pm$ 90	255 $\pm$ 106	156 $\pm$ 133	127 $\pm$ 127	395 $\pm$ 66
SLTMP	7.1 $\pm$ 1.2	7.9 $\pm$ 1.4	7.5 $\pm$ 1.4	8.3 $\pm$ 1.8	7.7 $\pm$ 0.5
SLWAT	12.5 $\pm$ 6.8	13.8 $\pm$ 1.7	10.5 $\pm$ 2.2	11.4 $\pm$ 3.0	38.8 $\pm$ 15.4
UNSTR	2.0 $\pm$ 0.4	2.2 $\pm$ 0.2	2.5 $\pm$ 0.3	2.5 $\pm$ 0.4	2.3 $\pm$ 0.1
ORG	7.4 $\pm$ 0.9	6.3 $\pm$ 0.7	6.5 $\pm$ 0.5	7.9 $\pm$ 1.5	8.0 $\pm$ 0.5

Table 2. (cont.)

	RACE	ROSE	ROSU	UMBR	MEAN
GRAV	35.3 ± 7.5	26.1 ± 3.0	11.9 ± 2.8	27.4 ± 3.3	23.7 ± 1.7
SAND	36.8 ± 6.1	34.8 ± 3.2	46.7 ± 4.0	36.3 ± 5.8	38.2 ± 1.7
SILT	25.7 ± 3.3	36.6 ± 3.0	38.9 ± 3.5	34.5 ± 4.5	35.4 ± 1.4
CLAY	2.2 ± 0.3	2.5 ± 0.4	2.6 ± 0.6	1.8 ± 0.3	2.7 ± 0.2
COVER	52.6 ± 7.1	66.3 ± 3.9	71.0 ± 6.1	58.7 ± 5.8	65.8 ± 2.3
CSDEV	10.6 ± 2.1	10.0 ± 1.5	8.3 ± 1.4	7.1 ± 1.2	8.7 ± 0.7
NTAXA	8.3 ± 0.9	8.9 ± 0.4	7.0 ± 0.4	8.6 ± 0.9	8.3 ± 0.2
CaCO <sub>3</sub>	0.1 ± 0.0	2.5 ± 2.0	0.2 ± 0.1	0.27 ± 0.1	4.1 ± 1.3
NO <sub>3</sub>	0.7 ± 0.2	1.6 ± 0.4	1.5 ± 0.2	3.3 ± 2.2	2.3 ± 0.4
NH <sub>4</sub>	6.3 ± 1.1	6.7 ± 1.2	4.6 ± 0.4	5.9 ± 1.0	6.3 ± 0.4
PO <sub>4</sub>	33.2 ± 7.0	19.6 ± 3.6	27.3 ± 4.6	26.0 ± 5.8	18.3 ± 1.7
SO <sub>4</sub>	10.6 ± 4.1	6.4 ± 2.2	3.7 ± 0.4	5.0 ± 0.7	9.5 ± 1.8
Ca	119 ± 21	146 ± 21	180 ± 21	160 ± 42	184 ± 21
Cu	3.9 ± 1.9	1.4 ± 0.2	1.5 ± 0.3	1.8 ± 0.8	2.1 ± 0.3
Fe	123 ± 21	68.2 ± 8.1	58.9 ± 11.3	61.3 ± 10.1	94.3 ± 11.1
K	8.9 ± 2.3	6.5 ± 0.8	9.9 ± 1.0	10.9 ± 1.9	8.1 ± 0.8
Mg	16.9 ± 4.7	14.4 ± 1.9	34.3 ± 6.2	14.9 ± 2.7	65.6 ± 26.8
Mn	84.2 ± 23.5	27.0 ± 4.9	22.0 ± 3.2	32.2 ± 9.3	30.1 ± 3.4
Na	1.0 ± 0.4	3.8 ± 3.1	1.0 ± 0.5	1.2 ± 0.5	4.3 ± 1.7
S	5.8 ± 0.2	6.3 ± 0.2	6.5 ± 0.4	6.3 ± 0.2	6.25 ± 0.1
Zn	2.9 ± 0.8	2.0 ± 0.6	1.3 ± 0.3	4.9 ± 1.4	2.3 ± 0.3

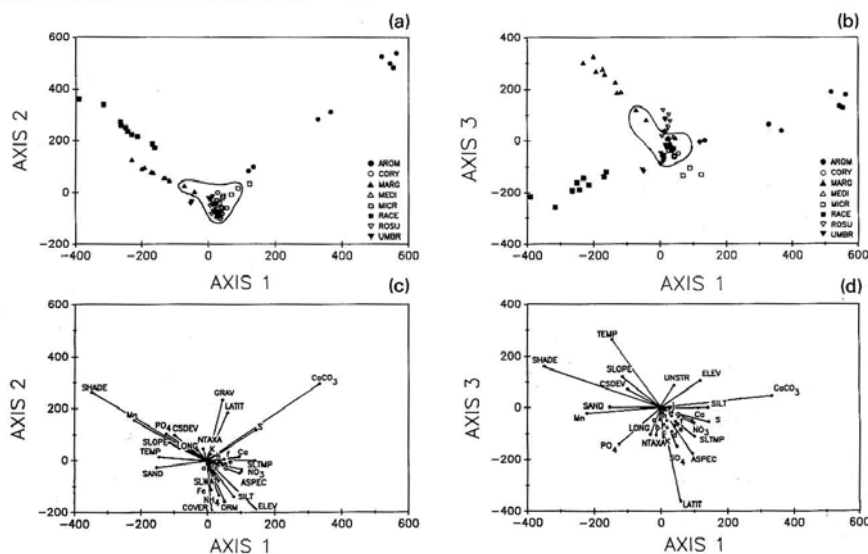


Fig. 5. The distribution of 77 study sites of eight amphimictic (sexual) species of *Antennaria* along CCA ordination axes 1 and 2 (a), and axes 1 and 3 (b), with corresponding environmental variables in (c) and (d). All sites for *A. rosea* are within the area surrounded by a continuous line. See text for guidance in interpretation of diagrams. Amphimictic taxa that were not clearly delimited in this analysis, i.e. *A. corymbosa*, *A. media*, *A. microphylla*, *A. rosulata*, and *A. umbrinella*, were analysed separately and the results are shown in Fig. 6. Environmental factor abbreviations are as those given in Table 2.



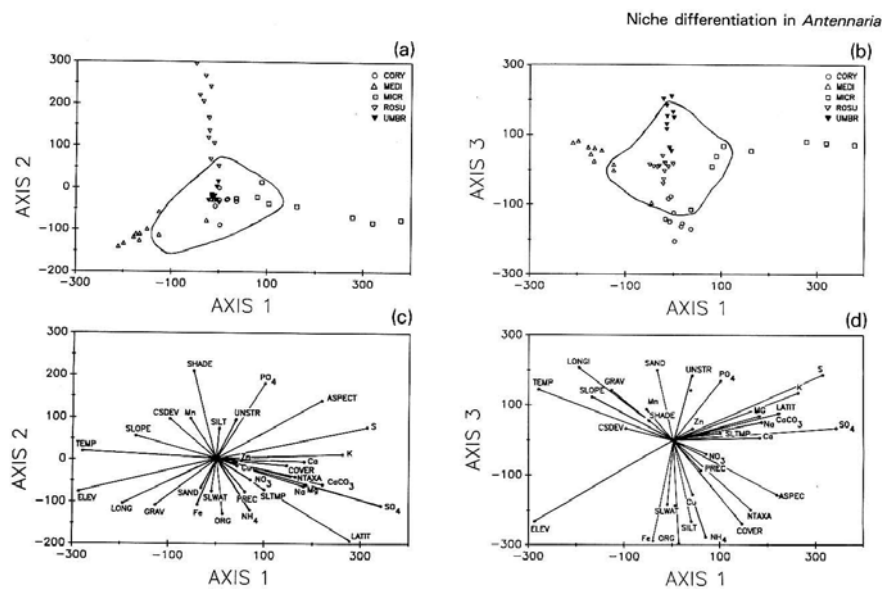


Fig. 6. The distribution of 47 study sites of five amphimictic species of *Antennaria* along CCA ordination axes 1 and 2 (a), and axes 1 and 3 (b), with corresponding environmental variables in (c) and (d). All sites for *A. rosea* are within the area surrounded by a continuous line. See text for guidance in interpretation of diagrams. Environmental factor abbreviations are as those given in Table 2.

results of this CCA. The per cent variance accounted for by the first three axes were 12.6, 11.6, and 10.8, respectively. The Monte-Carlo permutation option of CANOCO showed the ordination was significant at the 5% level. This second CCA clearly separated the remaining species sites on the basis of habitat. The niche of *A. rosea*, as defined by data from 24 sites, overlaps all of these five remaining sexual species to some extent and occupies a central position.

Sites containing *A. rosulata* are sunny and characterized by silty, moderately compacted, relatively non-organic soil with high PO<sub>4</sub> and relatively low Fe and NH<sub>4</sub> (Fig. 6). The community associates of *A. rosulata* most often include *Chrysothamnus vaseyi*, *Erigeron flagellaris*, *Eriogonum racemosum*, and *Lotus wrightii*. *Antennaria umbrinella* sites are delimited from the other groups of sites most satisfactorily along axis 3 (Fig. 6b). The *A. umbrinella* and *A. rosulata* sites are similar, but the taxa have allopatric ranges, *A. rosulata* occurring in the southern Rockies and *A. umbrinella* in the northern

Rockies (Figs 1 and 2). *Antennaria umbrinella* sites have soils that are dry, gravelly, sandy, compacted, high in Mn, PO<sub>4</sub> and Zn, and low in Fe, NH<sub>4</sub>, and organic matter. The typical associates of *A. umbrinella* include *Artemisia frigida*, *A. tridentata*, *Eriogonum umbellatum*, *Mahonia repens*, and *Purshia tridentata*, and the cover and the diversity of taxa in the communities is relatively low (Fig. 6).

*Antennaria microphylla* sites are discrete from those of the other *Antennaria* on the basis of a number of soil characters (high Mg, Ca, CaCO<sub>3</sub>, K, Na, S, and SO<sub>4</sub>; low in Mn). The sites are typically at low elevations on low slopes. Taxonomic diversity at *A. microphylla* sites is lowest of any of the other groups of sites and only *Trifolium repens* is consistently found at these sites. Several *A. microphylla* sites overlap the space occupied by *A. rosea* (Fig. 7b). One site for *A. microphylla* overlaps an *A. corymbosa* site and this is the result of the fact that they are parapatric sites within 5 metres of each other (Fig. 6a and b).

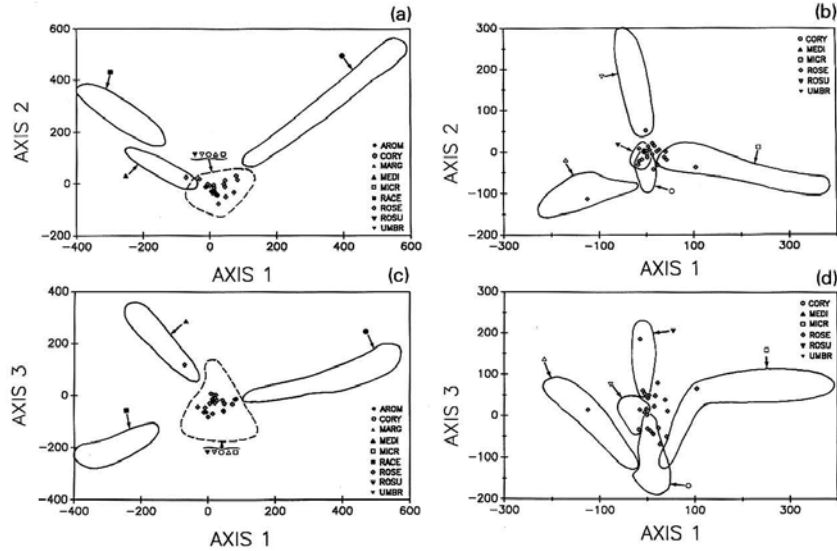


Fig. 7. The distribution of 24 study sites of *Antennaria rosea* along CCA ordination axes 1 and 2 (a and b), and axes 1 and 3 (c and d). Distribution of the sites of the amphimicts are outlined with solid or broken lines and are labelled with symbols that denote the taxa. The broken lines show the outline of several taxa, whereas the solid lines are individual taxa. Figures a and c correspond to the graphs in Fig. 5, while b and d match Fig. 6. Corresponding environmental lines are given in Figs 5 and 6. See text for guidance in interpretation of diagrams.

The *A. media* sites form a very discrete group (Fig. 6), except for one site which was atypically mesic (it actually co-occurred in the field with *A. corymbosa* at this site). Consequently this site, which is really more typical of *A. corymbosa*, actually clusters between the main clusters of the *A. corymbosa* and *A. media* sites (Fig. 6). The *A. media* sites tend to cluster at opposite ends of the spectrum of environmental characters from the ones for *A. microphylla* sites. *Antennaria media* localities are high elevation alpine on relatively steep slopes, characterized by moist soils with relatively high amounts of gravel, sand, and Mn, but low in Ca, CaCO<sub>3</sub>, K, Na, S, and SO<sub>4</sub>. A number of herbaceous perennials are often the community associates of *A. media*, namely *Ivesia lycopodioides*, *Penstemon heterodoxus*, *Saxifraga rhomboidea*, *Sibbaldia procumbens*, and *Silene acaulis*. *Antennaria corymbosa* sites are subalpine, but in contrast to *A. media* they have higher amounts of soil moisture and are generally on low to flat slopes. The organic soils on which *A. corymbosa* occurs are distinctive, being unconfined and containing high amounts of Cu, Fe,

NH<sub>4</sub>, and silt, but low amounts of PO<sub>4</sub> and Mn. The sites are characterized by having high amounts of total cover and a great diversity of community associates, which commonly include *Salix*, *Aster foliaceus*, *Caltha leptosepala*, *Potentilla diversifolia*, *Potentilla fruticosa*, *Viola adunca*, and *Veronica wormskjoldii*.

The results of the first discriminant analysis (DA) are presented in Table 3. The *A. rosea* sites were not given *a priori* group assignments because, based on the results of the CCAs, they apparently do not always have their own distinct niche. It is notable that from among the sexual taxa, 90% of the sites were correctly classified (Table 3). All of the sites of *A. aromatica*, *A. corymbosa*, *A. marginata*, and *A. racemosa* were correctly classified (Table 3). *Antennaria aromatica*, *A. marginata*, and *A. racemosa* have the most predictable habitats (Fig. 5; Table 3). Only eight sites of the sexual species out of 77 were not correctly classified.

Using DA, the *A. rosea* sites were assigned *a posteriori* to one of the sexual species groups. Approximately half of the sites were classified as *A. media* or *A. umbrinella*

**Table 3.** *A posteriori* classification from the discriminant analysis of the *Antennaria* study sites according to their species group. In the analysis, *A. rosea* was excluded from *a priori* group assignment. Species are labelled with the first four letters of their specific epithets. % = per cent correct classification. *N* = total number of study sites

TAXA	AROM	CORY	MARG	MEDI	MICR	RACE	ROSU	UMBR	%	<i>N</i>
AROM	8	0	0	0	0	0	0	0	100	8
CORY	0	10	0	0	0	0	0	0	100	10
MARG	0	0	10	0	0	0	0	0	100	10
MEDI	0	1	0	7	0	0	1	1	70	10
MICR	0	0	0	0	5	0	1	2	63	8
RACE	0	0	0	0	0	10	0	0	100	10
ROSU	0	0	0	1	0	0	10	0	91	11
UMBR	0	0	0	0	1	0	0	9	90	10
ROSE	2	1	2	5	2	3	2	7	—	24
TOTAL	10	12	12	13	8	13	14	19	90	101

(Table 3) with the remaining *A. rosea* sites assigned to the other six sexual taxa. It is interesting to note that both CCA and DA indicate that the *A. rosea* sites were most similar to those of *A. umbrinella*. Also DA assigns some *A. rosea* to *A. aromatica* (two sites) and *A. racemosa* (three sites), yet these are two taxa whose sites do not overlap the space of *A. rosea* in the CCA (Table 3; Fig. 5).

Of 24 *A. rosea* sites in the second DA, where *A. rosea* sites were given *a priori* group classification, 67% were correctly classified as *A. rosea* sites, while the other 33% were assigned to *A. marginata* (4%), *A. racemosa* (4%), *A. rosulata* (8%), and *A. umbrinella* (17%). This agrees with CCA (Fig. 7) in indicating that some *A. rosea* populations do occupy sites that are the same as or similar to those occupied by its progenitors.

## Discussion

### *Habitats of the sexual species*

The CANOCO ordination arranges sites such that those occupying similar niches appear in close proximity to each other. Each of the sexual species of *Antennaria*, including *A. aromatica*, *A. corymbosa*, *A. marginata*, *A. media*, *A. microphylla*, *A. racemosa*, *A. rosulata*, and *A. umbrinella*, appears to occur in a distinct niche (Figs 5, 6 and 7). 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. 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. For example, all *A. aromatica* sites are characterized by having soils with amounts of CaCO<sub>3</sub> that are several orders of

magnitude higher than those of any other site. The DA further supports the conclusion that most of the species occur in distinct habitats that are highly predictable.

The CCA also reveals which species occupy similar niches. *Antennaria marginata* and *A. racemosa* inhabit comparable habitats, yet several characters, such as elevation, slope and amounts of PO<sub>4</sub>, serve to separate them. Since the two species are geographically isolated, hybridization between them is prevented at the present time. This, however, does not preclude hybridization in the past, if their ranges overlapped during the last glacial period. Phylogenetic analysis indicates that *A. marginata* and *A. racemosa* are closely related (Bayer, 1990b) and this may explain why they occupy similar niches. *Antennaria rosulata* and *A. umbrinella* also occupy similar niches, but have allopatric ranges (Figs 1, 2 and 6). Their habitats can still be confidently separated based on organic matter, sand, and NH<sub>4</sub> contents of the soil as well as major community associates. Like *A. marginata* and *A. racemosa*, these two species cannot hybridize in nature because they presently have allopatric ranges. *Antennaria rosulata* and *A. umbrinella* are probably not very closely related based on a recent phylogenetic analysis (Bayer, 1990b). Some sites of *A. microphylla* and *A. rosulata* are also similar (Fig. 6b; Table 3) and the two have been noted growing in close proximity in southern Colorado (Bayer *et al.* CO-700 and CO-701). The ranges of these two species are mostly allopatric, the only regions where their ranges are sympatric are southern Colorado and extreme northern New Mexico. The two can be separated by several site characters including amounts of Ca, CaCO<sub>3</sub>, K, Mg, S, and SO<sub>4</sub> in the soil. *Antennaria microphylla* and *A. rosulata* are probably closely related phylogenetically (Bayer, 1990b). The above species pairs all have similar niches, but do not currently hybridize under natural conditions because they have allopatric

ranges. DA indicates that one site of *A. rosulata* (AZ-817; Table 3) should be classified as *A. media* and that one *A. media* site (CA-700; Table 3) should be classified as *A. rosulata* and although CA indicates that they have similar habitats based on a number of environmental characteristics, they can be easily separated by other abiotic factors as well as biotic ones. *Antennaria media* and *A. rosulata* are allopatric over much of their ranges and it is hard to conceive that their populations could overlap because of the great difference in the elevations at which they usually occur (Fig. 6). *Antennaria media* is alpine, whereas *A. rosulata* is montane and occasionally subalpine.

Some sympatric species pairs have similar niches, although spatially overlapping or conterminous ones are uncommon. The CCA and DA indicate that the niches 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*. *Antennaria corymbosa* and *A. microphylla* both tend to occur along streams or on floodplains of rivers. However, *A. corymbosa* occurs almost exclusively at higher elevations on moist, organic soil, while *A. microphylla* occurs at lower elevations on dry, non-organic soils that are high in mineral nutrients. In some cases the two habitats are adjoining (Taylor Reservoir, Gunnison Co., Colorado, Bayer *et al.* CO-864/CO-865; Tolland Lake, Gilpin Co., Colorado, Bayer *et al.* CO-462/CO-463). Two other species pairs have niches which may be neighbouring in sharp ecotonal areas of alpine/subalpine. Both *A. microphylla* and *A. umbrinella* occur at similar elevations, but *A. microphylla* favours floodplains or moist alkaline depressions, while *A. umbrinella* is found on the drier sagebrush covered hillsides. In ecotonal areas, for example mountain stream beds running through a surrounding very dry terrain, the two species can co-occur. Several such sites are known (Flint Mountains, Granite Co., Montana, Bayer *et al.* MT-736/MT-738). *Antennaria corymbosa*, occurring on moist, organic soil among willows with a high diversity of community associates and high vegetative cover, is found co-occurring with *A. media* growing on drier more mineral soil with low community associate diversity and low cover. In some alpine/subalpine areas where streams bearing snowmelt cross drier tundra, *A. corymbosa* and *A. media* can occur parapatrically. This occurs in some alpine areas (Beartooth Plateau, Carbon Co., Montana, Bayer *et al.* MT-705).

*Antennaria umbrinella* grows at a wide variety of elevations from lower montane to treeline, and it is in dry areas at treeline, that its niche may overlap with alpine *A. media*. DA points to the close similarity of one *A. media* site (Bayer *et al.* MT-722) to the typical *A. umbrinella* niche and indeed they grow in close

proximity at Goat Pass, Granite Co., Montana. Morphometric and isozymic analyses (Bayer, 1987b, 1989b) have consistently pointed to the morphological and genetic similarity between *A. media* and *A. umbrinella*. However, they seem to be ecologically well differentiated and this may serve to keep the taxa isolated enough as to maintain species integrity.

Several of the sexual taxa, including *A. aromatica*, *A. marginata*, *A. media*, and *A. umbrinella*, have both diploid and polyploid cytotypes. In general, diploid and polyploid cytotypes are morphologically and isozymically indistinguishable and it has been suggested that the polyploids are non-hybrid or autopolyploids (Bayer, 1987b, 1988, 1989b). The question can be asked whether diploid and polyploid populations of a species occupy distinct niches. Since the ploidy levels of many of the populations included in the CCA are known, it was possible to study their distribution on the graphs. After locating these populations on the diagrams it became evident that sites of diploid and polyploid populations within taxa do not form distinct groups. This supports the contention that the polyploid populations within the species are probably autopolyploids, as one might expect the non-hybrid polyploids would not occupy niches that are distinct from their diploid progenitor populations.

#### *Comparison of niche divergence among sexual taxa with morphological and isozyme divergence*

Among the sexual taxa, niche divergence tends to follow morphological divergence as analysed by Bayer (1987b). Those taxa that tend to be morphologically most distinct, such as *A. racemosa* and *A. marginata*, are also ecologically discrete. Morphometrics indicated that *A. aromatica*, *A. media*, 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 niches. Isozyme variation among the species follows a similar pattern to those of the morphological and niche divergence (Bayer, 1988, 1989b), although the taxa have not diverged at isozyme loci to the same degree as they have with respect to morphology or ecology.

Niche divergence among the species has obviously played an important role in the evolution of these species, as was suggested in Bayer (1987a). Ecological isolation along with geographic isolation are the primary mechanisms that help maintain species integrity and allow the species to continue to diverge. Reproductive isolating mechanisms evidently do not play an important role as barriers to hybridization among these sexual species of *Antennaria* because interspecific and later generation hybrids among all the taxa can be readily produced artificially in the greenhouse (Bayer, 1987a).

*Niche of Antennaria rosea and origins of the complex*

In the CCA, the *A. rosea* sites lie in the centre of the ordination space and overlap at least partially with all the sexual species except *A. aromatica* and *A. racemosa* (Fig. 7). Many *A. rosea* sites occupy niches that are very similar to those of their sexual progenitors. Some sites do however fall into distinct niches which are in between the groups of sites of the sexual species. These could be described as hybrid habitats, since they have sets of conditions that are intermediate between or among groups of sexual taxa. None of the *A. rosea* sites cover the range of abiotic conditions associated with the sexual taxa, i.e. they do not completely overlap the niche of any of their sexual relatives (Fig. 7). The CCA and DA support the hypothesis for the multiple hybrid origin of *A. rosea* proposed in Bayer (1990a), in that many sites of *A. rosea* occupy similar niches to their diploid progenitors, while others seem to occupy hybrid habitats that are intermediate between those of their sexual progenitors. Whether the intermediate niches occupied by some *A. rosea* represent niche space originally inhabited by their sexual progenitors or whether they have taken over the niche once occupied by species from other genera, cannot be determined from this analysis. It is also possible that some of the *A. rosea* clones occupy niches that are the result of geologically recent environmental disturbances such as glaciation, volcanic eruptions, etc. 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*.

*Evolutionary implications of niche 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 (Ehrendorfer, 1980; Levin, 1983; Fowler and Levin, 1984; Stebbins, 1984). 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 and Levin (1984) stress the importance of ecological factors, especially niche divergence, in establishment and persistence of polyploids. Stebbins (1984) has commended the studies of Johnson and Packer (1965, 1967, 1968) that emphasize the significance of ecological factors in delimiting the relative distribution of diploids and polyploids. Our study endeavours to contribute to the knowledge of how ecological factors influence the adaptive significance of allopolyploidy.

Although some data are available on the subject, much of it is anecdotal.

The 'secondary contact hypothesis' (Stebbins, 1984, 1985) places importance on secondary contact and subsequent hybridization between differentiated diploids to produce new, highly adaptive gene combinations which are subsequently maintained through polyploidy (and in the case of *A. rosea*, apomixis). 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. Hybridization among all the cytotypes has led to an enormous amount of variation in morphology among the descendent *A. rosea* clones. The current study 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 the diploids are morphologically uniform and ecologically separated (Ehrendorfer, 1980). The polyploids are morphologically diverse and occupy different habitats than their progenitors. He also asserted 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 seemed 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 our study of niche differentiation among species of *Antennaria* support the views of Ehrendorfer (1980) and Stebbins (1985), in that well over half of the *A. rosea* sites occupy niches not occupied by their progenitors and also the niches would seem to be moderate in comparison to those occupied by many of the progenitors.

Levin's conclusion that polyploidy may drive a population into a new 'adaptive sphere', and allow it to occupy niches beyond those of its progenitors (Levin, 1983) is supported by the present results. 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 niches and eventually leads to a saturation of most available niches 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 niches that are both unoccupied by an intermediate to those of its progenitors. Populations of *A. rosea* can therefore exist parapatrically with those of its progenitors. The idea that niche differentiation increases the probability of the coexistence of diploids and their polyploid derivatives (Fowler and Levin, 1984) is therefore supported by this study.

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