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American Journal of Botany, Volume 77, Issue 10 (Oct., 1990), 1313-1319.

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Amer. J. Bot. 77(10): 1313–1319. 1990.

PATTERNS OF CLONAL DIVERSITY IN THE ANTENNARIA ROSEA (ASTERACEAE) POLYPLOID AGAMIC COMPLEX[1]

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The perennial herbaceous species, *Antennaria rosea,* is a large, morphologically diverse, polyploid agamic complex that is widespread in the cordillera of western North America. The species consists of triploid and tetraploid, nonpseudogamous, gametophytic apomicts. Populations of *A. rosea* are gynoecious, consisting almost entirely of pistillate clones. Clonal diversity among 63 populations of *A. rosea* was studied over a large portion of its range. Isozyme electrophoresis utilizing four polymorphic enzyme systems detected 192 multilocus genotypes among the populations. Populations of *A. rosea* tend to be composed of one or a few genotypes (range 1–11; mean 3.5), and these genotypes usually occur in only one or a few localized populations. Geographic patterns of clonal diversity may be a result of frequent genesis of new clones in populations that occur in areas where sexual relatives of *A. rosea* donate compatible pollen to facultatively sexual apomicts. Populations from previously glaciated regions tend to have fewer clones per population than those from unglaciated portions of the range.

Studies of the clonal structure of apomictic plant populations have received revitalized interest in the past decade as a result of electrophoretic techniques, which allow us to better assess the genotypic composition of populations. A well-established general belief has been that asexually reproducing species lack genetic diversity and can be considered as evolutionary "dead-ends." This belief has come under criticism as a result of some recent investigations, summarized in a recent review by Ellstrand and Roose (1987). Various studies have shown that asexually reproducing plants can be much more genetically diverse than originally thought. Despite recent evidence to the contrary, the idea of agamic species as evolutionary dead-ends prevails, and the reviews by Ellstrand and Roose (1987) and Bierzychudek (1985) have pointed to the lack of adequate studies of clonal diversity in asexual plants and have stressed the need for additional studies.

Because *Antennaria* Gaertn. (Asteraceae; tribe Inuleae) is dioecious, agamospermous taxa can be readily identified by the lack of staminate clones, and sex ratios in populations provide a valuable, although not infallible, means of assessing the frequency of different reproductive modes within populations (Bayer and Stebbins, 1983). Asexual reproduction in *Antennaria* occurs through both agamospermy and vegetative spreading via stolons. Many ecological, taxonomic, and phylogenetic studies have already been conducted within the genus (Bayer and Stebbins, 1982, 1983, 1987; Bayer, 1984, 1987b, 1989a, b, c; Bayer and Crawford, 1986; Michaels and Bazzaz, 1986) and have provided necessary background information.

Antennaria rosea Greene is a widespread polyploid occurring throughout western North America from New Mexico to Alaska with disjunct populations in eastern North America near James Bay, Lake Superior and in Atlantic Canada (Bayer, 1989c; Fig. 1). The species is composed of a series of triploid and tetraploid gametophytic apomicts (Bayer, 1987a, 1989c). Pseudogamy has not been reported for the genus (Nogler, 1984), and heads of *A. rosea* develop fertile seeds when isolated from potential pollen sources (Bayer, unpublished data). Most populations are composed entirely of pistillate plants, staminate plants being exceedingly rare; fewer than 25 staminate clones were seen dur-

[1] Received for publication 26 October 1989; revision accepted 25 May 1990.

The author thanks Glenn Bilodeau, Rob DeLuca, Mark Joncas, Klaus Lackschewitz, Dan Lebedyk, Helen Michaels, Ledyard Stebbins, and Krystyna Urbanska for accompanying him in the field on various occasions; and Spencer Barrett, Mark Dale, Norman Ellstrand, David Innes, LuDean Marvin, Helen Michaels, Brett Purdy, and Ledyard Stebbins for critical reviews and helpful comments on earlier versions of the manuscript. This research was supported by the Natural Sciences and Engineering Research Council of Canada (NSERC grant #A3797) and by University of Alberta Central Research Fund grants #55-47930 and #55-48947.

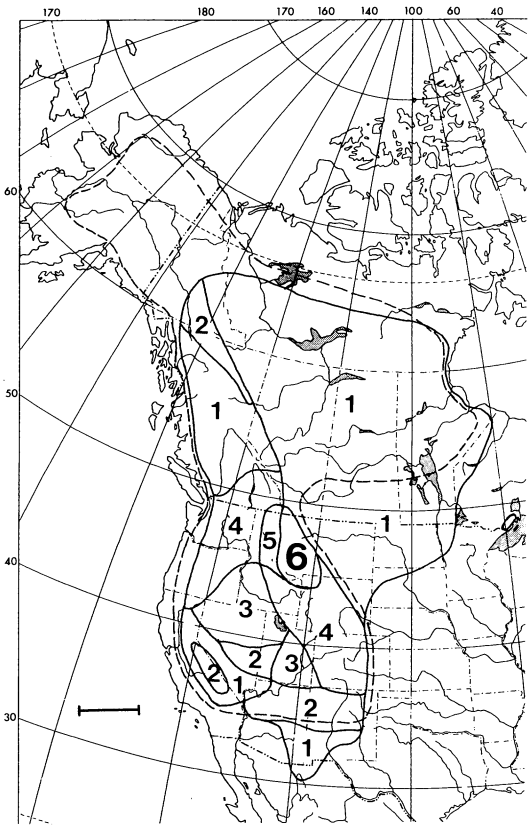

Fig. 1. Map of western North America illustrating ranges of *Antennaria rosea* and its sexual relatives. The range of *A. rosea* is indicated by a dashed line. The ranges of the sexual species are indicated by solid lines, and numbers inside each region are the sexual diversity indices, which are simply the number of sexual species that are sympatric within each region. Bar = 500 km.

ing seven summers of field observations of over 200 populations (Bayer, 1989c, unpublished observations).

There is considerable morphological variation within the species (Bayer, 1990) resulting from the diverse hybrid origin of the species complex (Bayer, 1989a, 1990). It is well established that agamic complexes arise through hybridization among related sexual taxa followed by polyploidization (Gustafsson, 1947; Nogler, 1984; Bayer, 1987a). Most apomicts are found among outcrossing, perennial plants because hybridization and longevity are necessary for both the acquisition of genes for apomixis as well as the evolution of polyploidy in the hybrids (Gustafsson, 1947). The *A. rosea* complex may be the result of hybridization among as many as eight sexually reproducing diploid and tetraploid species of *Antennaria,* including *A. aromatica* Evert, *A. corymbosa* Nels., *A. marginata* Greene, *A. media* Greene (including *A. pulchella* Greene), *A. microphylla* Rydb., *A. racemosa* Hook., *A. rosulata* Rydb., and *A. umbrinella* Rydb. (Bayer, 1989a, c, 1990).

The objective of this paper is to describe the clonal diversity within and among populations of *A. rosea* throughout its range. The factors that might be responsible for any detected patterns will then be explored. Patterns of clonal variation will be compared with geographic factors to determine whether an association exists between clonal diversity and latitude, longitude, elevation, glacial history, and/or presence of sexual relatives.

MATERIALS AND METHODS

The taxonomic cirscumscription of *A. rosea* is outlined in Bayer (1989c). Throughout this paper the words clone and apomict are used interchangeably and refer to an individual lineage reproduced asexually by apomixis or vegetatively via stolons. Apomixis refers to asexual seed production (agamospermy or gametophytic apomixis), not vegetative reproduction by stolons. The terms pistillate and staminate refer to the sporophytes that produce only female and only male gametophytes, respectively.

Sixty-three populations of *A. rosea* were sampled from throughout the range of the species from 36°14′N to 62°37′N latitude and 105°25′W to 135°08′W longitude. An appendix presenting the population locality data and population designations used throughout the paper is available at the author's discretion. The elevation of sites ranged from 579 to 3,719 m. An effort was made to obtain a representative set of populations from across *A. rosea*'s wide range. Populations of *A. rosea* are rare at the margins of the range, in glaciated Canada and Alaska, in the moist Pacific coastal forests, and in the desert mountain ranges of the Great Basin. Nonetheless, a large portion of the range of the species was sampled, with a fairly even distribution of sites (Fig. 2). Herbarium voucher collections at the University of Alberta Vascular Plant Herbarium document the morphological diversity within each population.

In general, individuals of *A. rosea* form relatively small, spatially distinct aggregations, so individuals can be confidently identified. Ramets were removed from up to 35 individual plants from each population. Most populations were composed of fewer than 35 aggregations, and consequently, every clone in the population was sampled. In large populations, an effort was made to choose aggregations that were morphologically different from one another to

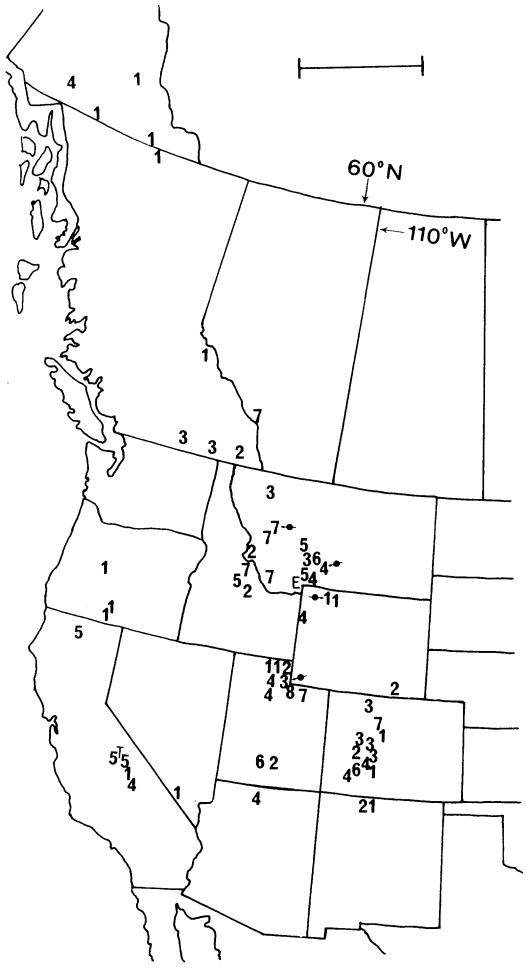

Fig. 2. Map of western North America showing the geographic distribution of 63 populations of *Antennaria rosea* used in this study. Each population is represented by a number or letter indicating the number of multilocus genotypes detected in each population. One to nine clones per population are indicated by the corresponding numbers, while populations with ten and 11 clones are represented by the letters "T" and "E," respectively. The four triploid populations are marked by solid circles with arrow pointing at them, whereas the 59 tetraploid populations are not tagged. Bar = 500 km.

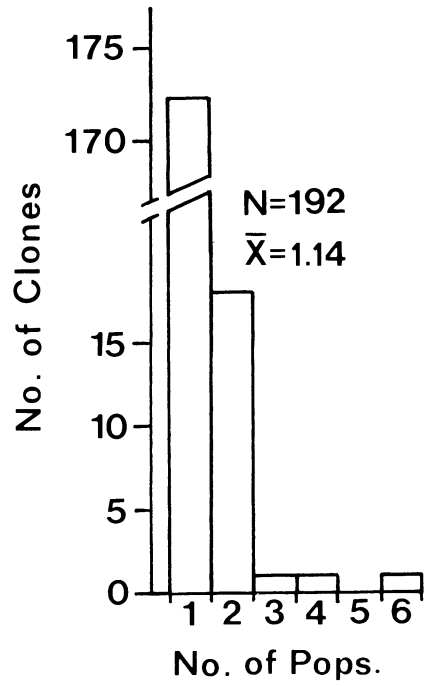

Fig. 3. Histogram illustrating the frequency distribution of 192 unique multilocus genotypes among the 63 populations of *Antennaria rosea*. No. of Pops. = number of populations in which each unique clone was detected. Mean number of populations that each clone occurred in was 1.14.

maximize the amount of clonal diversity detected. Several meters were allowed between the sampling of consecutive plants in large populations to further assure that different clones were being sampled. Ramets were transported to the phytotron of the University of Alberta for cultivation and subsequent analysis.

Electrophoretic procedures were identical to those in Bayer (1988). A total of 1,063 individuals were assayed (average of 16.9 [range seven to 35) individuals per population). Kendall's coefficient of rank correlation (Zar, 1984) indicated that the number of clones detected per population was not significantly correlated with the sample size (tau = 0.0747, $P = 0.2124$). Previous work with *A. rosea* had shown that four loci were polymorphic, readily interpretable, and had predictable levels of activity. Consequently, acid phosphatase (*Acp-1*), leucine aminopeptidase (*Lap-1*), phosphoglucoisomerase (*Pgi-3*), and triose-phosphate isomerase (*Tpi-3*) were the loci used to assign a multilocus genotype to each plant. Ploidy levels were determined for each population using techniques outlined in Bayer (1984), so that allozyme dosages of unbalanced heterozygotes could be properly scored. As discussed in Bayer (1989a), loci were scored based on the assumption of trisomic inheritance for triploid populations and tetrasomic for tetraploids. Balanced heterozygotes in tetraploid clones were scored as having two copies of each allele, unbalanced heterozygotes as having one and three copies of the respective alleles. All heterozygotes in triploid clones are unbalanced having two copies of one allele and one copy of the other.

Clonal diversity was assessed by calculating the total number of unique multilocus genotypes, as well as the distribution of those genotypes among the populations. The overall

genotypic frequency of each apomict was determined by dividing the number of times that the clone was encountered in all populations by the total number of individuals surveyed. The mean air distance among populations containing the same clone was calculated as an average distance among all pairwise comparisons. The number of clones per population was determined and the relative proportions of monoclonal and polyclonal populations calculated. The "proportion distinguishable" value of Ellstrand and Roose (1987) was determined by calculating the number of clones detected in a population divided by the number of ramets assayed in that population.

Regression analyses (Norusis, 1988; SPSS-pc) were used to look for association between clonal diversity and geographic factors. Linear regressions were calculated where the dependent variable, number of clones per population, was regressed on each of the three independent variables: elevation, latitude, and longitude.

The number of sexual progenitor species that are sympatric with *A. rosea* populations ranges from one to six (Fig. 1). This is the number of possible sexual species that could act as pollen donors to a population of *A. rosea* in a given region. The area of highest sexual diversity is western Montana (Fig. 1). The distance in air kilometers of each population from this center of sexual diversity was calculated. Linear regression (Norusis, 1988; SPSS-pc) was employed to determine whether the sexual progenitor number and distance from the area of maximum sexual diversity were good predictors of clonal diversity in populations. Kendall's tau-b (Norusis, 1988; SPSS-pc; Zar, 1984) was calculated to test the relationship between the sexual progenitor number and distance from the center of maximum sexual diversity. Finally, a log likelihood ratio (G test; Zar, 1984) was used to determine if there is a significant difference in clonal diversity between glaciated and unglaciated regions, independent of sexual progenitor number.

RESULTS

Figure 2 shows the geographic distribution of the populations and the numbers of distinct clones within each. The geographic distribution of the number of sexual taxa related to and sympatric with *A. rosea* within each region is illustrated in Fig. 1. The range in distance among populations surveyed was 12 to 3,175 km (Fig. 2).

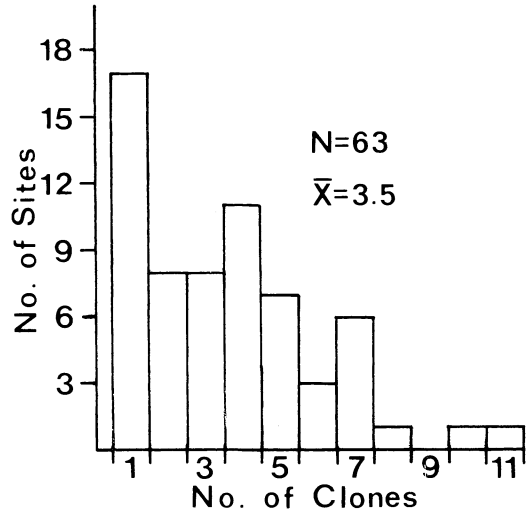

Fig. 4. Histogram showing the number of clones found in each of the 63 populations of *Antennaria rosea*. No. of Sites = the actual number of sites containing a given number of clones. Mean number of clones per population was 3.5.

Six alleles were detected for both *Pgi-3* and *Tpi-3*, five alleles at *Lap-1*, and three at *Acp-1*. A total of 192 clones was detected among the 1,063 individuals from the 63 populations that were surveyed. Genotypic frequencies of the apomicts range from 0.0009 to 0.0489 (mean = 0.016). Figure 3 demonstrates that 89.1% (171/192) of the apomicts are very restricted, occurring in only one population. The remaining 10.9% of the clones occurred in two to six populations (Fig. 3), and the average distance among populations containing the same clone is 910 km (range 54 to 2,730 km). The average number of populations that each apomict occurred in is 1.14 (Fig. 3). Additional appendices listing the genotype of each clone, the genotypic frequency of each clone, the number of populations in which each clone occurred, and the clonal composition of each population, are available from the author on request.

Clonal diversity within populations ranges from one to 11 multilocus genotypes per population (mean = 3.5 clones per population; Fig. 4). Twenty-seven percent of the populations were monoclonal and 73% were polyclonal. The mean proportion distinguishable value ranged from 0.037 to 1.0 (mean = 0.253) and is a good indicator of the clonal diversity in *A. rosea* as it is related to sample size.

Linear regressions showed that neither elevation ($F = 1.86$, $F_{0.05(2),1,61} = 5.29$), latitude ($F = 1.34$), nor longitude ($F = 1.73$) are significant predictors of the number of multilocus

genotypes within populations. However, both the sexual progenitor number ($F = 9.14$, $F_{0.05(2),1,61} = 5.29$) and distance from the area of maximum sexual diversity ($F = 6.59$) were significant predictors of the number of clones per population. The influence of ploidy level on the distribution of clonal diversity is probably not a factor since the apomicts are overwhelmingly tetraploid, with triploids accounting for only 2% of the clones. In general, populations of *A. rosea* that are sympatric with one or very few sexual species and are a great distance from the center of sexual diversity in western Montana have lower numbers of apomicts than populations that are sympatric with greater numbers of sexual species or near the center of sexual diversity (Fig. 1). Also, populations in areas that were glaciated by continental glaciers during the Pleistocene (based on Prest, 1984) tended to have fewer clones per population than those that occurred in areas that were free of continental ice sheets ($G = 65.1$, $\chi^2_{0.05,9} = 16.92$) (Fig. 2).

DISCUSSION

This study uncovered a remarkable amount of clonal diversity within *A. rosea* as a whole, especially considering that the number of clones discerned is undoubtedly a conservative estimate of the actual number of clones per population. More genotypes would probably have been detected if additional polymorphic loci had been available. The number of clones detected is generally more a function of numbers of loci used than sample size (Ellstrand and Roose, 1987). Even using only four loci, the total number of genotypes found exceeded that for nearly all the studies reviewed by Ellstrand and Roose (1987). It is possible that the estimates of clonal diversity in the larger populations (greater than 35 clones) of *A. rosea* are larger than those found in other species because the sampling employed in this study attempted to maximize the amount of clonal diversity detected. In smaller populations, unabridged diversity is reported, because all clones were sampled.

Ellstrand and Roose (1987) provided a summary of studies that have investigated clonal diversity in plants where sexual reproduction is rare or absent, including an alga, a cryptogam, a gymnosperm, and angiosperms. The number of studies is small (the number of species is even smaller), and those have mostly assayed only a few populations (mean 12.5); only three have assessed more than 20 populations. It is surprising that so few studies investigating clonal diversity in plants have been undertaken, especially considering the large number of plant groups (Fryxell, 1957) that maintain some form of asexual reproduction. The results from *A. rosea* are best compared to those obtained for *Taraxacum* (Lyman and Ellstrand, 1984; Ford and Richards, 1985; Mogie, 1985; Van Oostrum, Sterk, and Wijsman, 1985; Hughes and Richards, 1988) because the species are perennials in the same family with similar evolutionary patterns (Bayer, 1987a). However, variations in population sizes and numbers, differences in sampling strategies, as well as absence of some genetic statistics, sometimes make meaningful comparisons between *A. rosea* and *Taraxacum* difficult.

The mean proportion of clones distinguishable (0.253) is higher than those values obtained in most other studies (Ellstrand and Roose, 1987). The high proportion of polyclonal populations (73%) is similar to the average obtained for other plant studies (77%; Ellstrand and Roose, 1987) and animal studies (Parker, 1979). The distribution of apomicts among populations indicates that 89.1% are very restricted in their distribution, whereas only 10.9% of the apomicts are limited in their distribution (Fig. 3). Ellstrand and Roose (1987) reported that an average of 75.8% of the genotypes in their survey were very restricted. The higher proportion of distinguishable clones and higher frequency of very restricted clones may indicate that *A. rosea* clones are more numerous but are geographically more restricted than those of other apomicts.

The number of multilocus genotypes per population (mean = 3.5 clones per population; Fig. 4) is lower than values obtained for most plant studies (16.1; Ellstrand and Roose, 1987) but similar to those found in populations of *Taraxacum* and numerous animal studies (Parker, 1979). This difference, however, could be attributable to the smaller population size characteristic of many populations of *A. rosea* or poorer dispersal and establishment when compared to most other asexual plant populations. Smaller populations would tend to have fewer clones than large ones. None of the apomicts were widespread in frequency, defined as occurring in more than 75% of the populations (criterion of Ellstrand and Roose, 1987). The major difference between *A. rosea* and the results from other plant studies is that populations of *A. rosea* appear to be composed of a few rather localized genotypes, although the relatively low number of populations surveyed in most of the other studies makes meaningful comparisons difficult. *Antennaria rosea* is similar to the cladoceran, *Daphnia,* not only with

respect to number of clones per population and the distribution of individual clones among populations, but also geographic patterns of distribution of polyploidy and apomixis within species in North America (Weider, Beaton, and Hebert, 1987; Beaton and Hebert, 1988; Hebert, Ward, and Weider, 1988).

The evolution of new apomictic clones in *A. rosea* is paradoxical. If *A. rosea* is obligately agamospermous, then how do new clones arise? Perhaps some clones of *A. rosea* occasionally produce sexual embryo sacs (facultative sexuality) and these are subsequently fertilized by compatible pollen from nearby sexual progenitors. This would explain the triploid apomicts as hybrids of tetraploid *A. rosea* and the sympatric sexual diploids. Many of the tetraploid apomicts could be hybrids between tetraploid *A. rosea* and sympatric tetraploid sexuals. Unique marker allozymes are supportive of the fact that *A. corymbosa, A. microphylla,* and *A. umbrinella* are among the parents of the *A. rosea* complex (Bayer, 1989a). Fourteen of the 17 populations of *A. rosea* containing clones that have these unique alleles are from sites that overlap the range of the particular sexual species containing the same marker alleles, which further strengthens this argument. Geographic patterns of clonal diversity in *A. rosea* may be a result of more frequent genesis of new clones in populations that co-occur in areas where sexual relatives of *A. rosea* contribute large amounts of compatible pollen to facultatively sexual clones. Clausen's "Henry Ford" or "model T" hypothesis (Clausen, 1954; Marshall and Brown, 1981) concerning the adaptive significance of apomixis may apply to the case of *A. rosea,* where facultative sexuality continually supplies the necessary genotypes to be tested, but only the most successful ones are "reproduced authentically" and continuously via apomixis. Facultative amphimicts may play a very important role in the maintenance of clonal diversity in the *A. rosea* complex.

This study also shows that clonal diversity declines with distance from the center of distribution. Lower numbers of apomicts in populations at the margins of the ranges could have several possible causes. First, these populations could be more recently established. Secondly, populations near the center of the range, where the largest numbers of sexual species occur, could be more clonally diverse because new apomicts arise more frequently as a result of facultative sexuality in some clones of *A. rosea.* This might also account for the sporadic occurrence of staminate *A. rosea* plants near the center of the range (Bayer, unpublished observations). Also, pistillate triploid *A. rosea* occurs mostly near the center of the range of the species (Bayer, 1987a; Bayer and Stebbins, 1987; Fig. 2). Finally, even if rates of genesis of new apomicts are the same, populations in the center of the range could be more diverse if selection in these regions is less intense. Consequently, stronger directional selection in marginal sites along with balanced selection in central sites perhaps accounts for the observed patterns of clonal diversity.

It has been proposed that *A. rosea* survived the Pleistocene south of the glacial margin and migrated north to the arctic after glacial retreat (Bayer, 1990). The sexual progenitors, for the most part, have not migrated into the previously glaciated terrain (Bayer, 1990). There is a significant negative correlation between clonal diversity and glaciation. It is possible that some clones of *A. rosea* survived the Pleistocene in unglaciated portions of Alaska and Yukon Territory, and a survey of populations from this region could provide valuable information about the phytogeographic history of the complex, as well as the effect of glaciation on clonal diversity.

In conclusion, populations of *A. rosea* tend to be composed of one or a few genotypes. These genotypes usually occur in only one or a few populations, supporting the strawberry-coral model of clonal population structure proposed by Williams (1975). The notion that weedy apomictic species are composed of widespread genotypes (Baker, 1974) doesn't appear to be supported by the data from *A. rosea* populations. Decreasing clonal diversity between northern and southern latitudes seems to be partially sustained because northern populations of *A. rosea* are generally less diverse than their southern counterparts, based on significant differences in numbers of clones from populations in glaciated vs. unglaciated regions.

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

patible pollen donors, new apomicts might arise through sexual reproduction.

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