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PATTERNS OF CLONAL DIVERSITY IN GEOGRAPHICALLY MARGINAL POPULATIONS OF ANTENNARIA ROSEA (ASTERACEAE: INULEAE) FROM SUBARCTIC ALASKA AND YUKON TERRITORY

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Antennaria rosea (Asteraceae: Inuleae) is a herbaceous perennial that reproduces by gametophytic apomixis and is widespread in the cordillera of western North America, ranging from New Mexico to Alaska. In the overall pattern of population structure in *A. rosea,* the majority of the populations are polyclonal, although the average number of clones per population is relatively small ($\bar{X} = 3.1$). In general, clones are restricted to one or two populations ($\bar{X} = 1.1$) and, therefore, very few widespread clones exist. The subarctic populations are characterized by relatively low amounts of clonal diversity when compared with those from southern latitudes ($\bar{X} = 2.0$/population). Clonal diversity is negatively correlated with latitude, longitude, and elevation of the sites. It seems unlikely that *A. rosea* survived the last glacial episode in the northern glacial refugium, Beringia, and a more likely scenario for the phytogeographic pattern of clonal diversity is one that envisions *A. rosea* surviving the Wisconsinan south of the glacial margin or perhaps arising in the same region at the end of the Wisconsinan. New clones probably arise via crossing of facultatively apomictic clones of *A. rosea* to their sexual progenitors. As most of the eight sexual progenitor taxa are absent from the north, new clones cannot easily arise there. The lack of clonal diversity in the subarctic and arctic could be the result of a combination of recent migration and lack of sexual progenitors in the region.

Introduction

Antennaria rosea Greene (Asteraceae: Inuleae) is a morphologically diverse herbaceous perennial that is widespread in the cordillera of western North America, occurring from New Mexico to Alaska with disjunct populations in eastern North America near James Bay, Lake Superior, and in Atlantic Canada (BAYER 1989*b*). The *A. rosea* polyploid complex is of multiple hybrid origin from perhaps as many as eight sexually reproducing diploid and tetraploid species of *Antennaria,* including *A. aromatica* Evert, *A. corymbosa* Nels., *A. marginata* Greene, *A. pulchella* Greene (including the polyploid, *A. media* Greene), *A. microphylla* Rydb., *A. racemosa* Hook., *A. rosulata* Rydb., and *A. umbrinella* Rydb. (BAYER 1989*a,* 1989*b,* 1990*a*). The species is composed of triploid and tetraploid, nonpseudogamous, gametophytic apomicts (BAYER 1990*b*). Populations of *A. rosea* are gynoecious, consisting almost entirely of pistillate clones; fewer than 25 staminate clones were seen during seven summers of field observations of more than 200 populations (BAYER 1990*b*).

The first article in this series revealed a tremendous amount of clonal variation in 63 populations of *A. rosea* (BAYER 1990*b*). Clonal diversity among the populations of *A. rosea* was studied over the large, central portion of its range, and sampling was quite limited in the northern portion of its range in Yukon and Alaska (BAYER 1990*b*). Isozyme electrophoresis utilizing four polymorphic enzyme systems revealed 192 multilocus genotypes among the 63 populations (BAYER 1990*b*). Populations of *A. rosea* tend to be composed of one or a few genotypes (range 1–11; $\bar{X} = 3.5$; BAYER 1990*b*). Individual genotypes usually occur in only one or a few populations (BAYER 1990*b*).

Geographic patterns of clonal diversity may be a result of the regular production of new clones in populations in areas where sexual relatives of *A. rosea* contribute compatible pollen to facultatively sexual apomicts (BAYER 1990*b*). Populations from previously glaciated regions tend to have fewer clones per population than those from southern unglaciated portions of the range, although sampling from the glaciated region has been somewhat limited (BAYER 1990*b*). The sexual progenitors, for the most part, have not migrated into the previously glaciated terrain (BAYER 1990*a*). 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*a*). However, it is possible that some clones of *A. rosea* have 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.

The primary objective of this article is to describe the clonal diversity within and among populations of *A. rosea* from the northern portion of its range. Data from the current study will then be incorporated with those from the initial study (BAYER 1990*b*) to reanalyze clonal diversity in the complex in view of the additional data. The

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TABLE 1

LOCALITY DATA FOR 21 POPULATIONS OF ANTENNARIA ROSEA FROM SUBARCTIC NORTH AMERICA

Canada, Yukon Territory:
- Fort Selkirk quad, MacMillan Range, along Klondike highway, 6.2 km N of the Willow Creek crossing; 63° 04′N, 136° 28′W; 670 m; YK-89036
- Klondike quad, South Ogilvie Mountains, along the Dempster highway, 16.5 km N of junction with the Klondike highway; 64° 05′N, 138° 34′W; 760 m; YK-89056
- Midnight Dome summit, near Dawson City; 64° 04′N, 139° 22′W; 910 m; YK-89101
- Pelly River quad, McKenzie Mountains, Selwyn Range, along North Canol road, 7 km E of Boulder Creek crossing; 62° 50′N, 130° 45′W; 980 m; YK-89026
- Tatchun Hills, along Campbell highway, 2.4 km W of Bear Feed Creek; 62° 10′N, 135° 08′W; 630 m; YK-89035
- Along Silver trail between Mayo and Minto Bridge; 63° 40′N, 135° 50′W; 580 m; YK-89040
- Along Silver trail, road to Keno, about 500 m N of turnoff to South McQueston; 63° 45′N, 135° 51′W; 800 m; YK-89055
- St. Elias quad, near Bear Creek Summit, Bear Creek road, about 100–500 m SW of the Alaska Highway; 60° 55′N, 137° 48′W; 1,010 m; YK-89105
- Whitehorse-Teslin quad, Pelly Mountains, along South Canol road, about 400 m N of Lower Lapie River crossing #1; 61° 43′N, 133° 04′W; 990 m; YK-89019
- Along South Canol road, about 21.7 km from its junction with the Alaska Highway; 60° 34′N, 138° 05′W; 880 m; YK-89107
- Floodplain along Wolf Creek at Alaska Highway crossing, about 16 km SE of Whitehorse; 60° 36′N, 134° 48′W; 763 m; YK-89110
- Wolf Lake–Watson Lake quad, along Campbell highway, 11.3 km N of Watson Lake (townsite); 60° 09′N, 128° 56′W; 630 m; YK-89001
- Along Campbell highway, .8 km E of Van Vibber Creek and 29 km W of turnoff to Finlayson Lake; 61° 37′N, 130° 15′W; 850 m; YK-89003
- Along Campbell highway, .5 km W of Mink Creek crossing; 61° 44′N, 131° 19′W; 820 m; YK-89005

U.S.A., Alaska:
- Anchorage quad, Talkeetna Mountains, Eureka summit along the Glenn highway; 61° 55′N, 147° 08′W; 1,010 m, AK-89020
- Chugash State Park, Eklutna valley, about 1.5 km E of Eklutna campground; 61° 08′N, 149° 05′W; AK-89042
- Big Delta quad, bluffs along Salcha River at the Richardson highway crossing; 64° 28′N, 146° 58′W; 170 m; AK-89149
- Gulkana quad, along Glenn highway, 1.4 km E of Tolsona Lake turnoff; 62° 06′N, 146° 02′W; 660 m; AK-89012
- Mt. Hayes quad, Alaska Range, near the shore of Fielding Lake; 63° 12′N, 145° 40′W; 910 m; AK-89159
- Along Denali highway, 19.1 km E of the Tangle River crossing and 16.8 km E of Round Tangle Lake; 63° 05′N, 145° 41′W; 960 m; AK-89181
- Tanacross quad, Alaska Range, along clearwater creek access road, about 28.5 km N of the Tok River crossing; 63° 14′N, 143° 05′W; 570 m; AK-89001

NOTE.—Presented are topographic map quadrangle, brief locality description, latitude, longitude, elevation (m above sea level), and collection numbers. Voucher specimens are at ALTA.

factors that might be responsible for any detected patterns will then be explored, and patterns of clonal variation will be compared with geographic factors to ascertain whether an association exists between clonal diversity and latitude, longitude, elevation, glacial history, and/or presence of sexual relatives. The phytogeographic history of *A. rosea* will be augmented based on clonal diversity data from the subarctic populations.

Material and methods

The taxonomic circumscription of *Antennaria rosea* is presented in BAYER (1989*b*). Throughout this article, "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. "Pistillate" and "staminate" refer to the sporophytes that produce only female and only male gametophytes, respectively. The adjective "current" refers to the 21 populations from the subarctic that are the subject of this investigation; "previous" refers to the 63 populations from the first study (BAYER 1990*b*), and "expanded," to all 84 studies together as one large data set.

Twenty-one populations of *A. rosea* were sampled throughout the range of the species in Alaska and Yukon from 60° 09′ N to 64° 28′ N latitude and 128° 56′ W to 149° 05′ W longitude, whereas the elevation of sites ranged from 170 to 1,010 m (table 1; fig. 1). Populations of *A. rosea* are less frequent at the margins of the range, in glaciated subarctic Canada and Alaska; nevertheless, a fairly even distribution of sites has been surveyed (fig. 1). Herbarium voucher collections at ALTA document the morphological diversity within each population.

Sampling methods and electrophoretic protocols were identical with those outlined in BAYER (1990*b*); therefore, only a brief account will be provided. Ramets were removed from up to 35 individual plants from each population. Many populations were composed of fewer than 35 plants, and consequently, every clone in the population was sampled. Ramets were brought to the phytotron of the University of Alberta for cultivation and subsequent analysis. Fresh leaf material was used for electrophoresis.

A total of 560 individuals ($\bar{X} = 26.7$; range = 9–32) were examined. Kendall's coefficient of rank correlation (ZAR 1984) showed that the number of clones detected per population was not significantly correlated with the sample size ($\tau = .0247$, $P = .447$). The previous study of clonal diversity in *A. rosea* (BAYER 1990*b*) had shown that four loci were most useful in assigning multilocus genotypes to individuals because they were poly-

morphic, 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 provide a genotype for each plant in this study. Chromosome numbers were determined for each population (BAYER 1984) so that allozyme dosages of unbalanced heterozygotes could be properly scored. As discussed in BAYER (1989*a*, 1990*b*), loci were scored on the assumption of tetrasomic inheritance.

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 unique multilocus genotypes were also compared to those from the previous study (BAYER 1990*b*) to determine whether any of them occurred in the 63 previously surveyed 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 were calculated; these were subsequently added to those of the previous study (BAYER 1990*b*) to provide these values for an expanded data set. 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. The proportion distinguishable values for the expanded study (84 populations) were also calculated.

Regression analyses (SPSS-pc; NORUSIS 1988) were used to look for associations between clonal diversity and geographic factors. These analyses were carried out only on the expanded data set (84 populations: 63 from BAYER 1990*b* and 21 from the current study). For linear regressions, number of clones per population (the dependent variable) 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. 2). This is the number of possible sexual species that could act as pollen donors to a population of *A. rosea* in a given region (fig. 2). The distance in air kilometers of each population from this center of sexual diversity was calculated. Linear regression (SPSS-pc; NORUSIS 1988) was employed to determine whether the sexual progenitor number and distance from the area of maximum sexual diversity

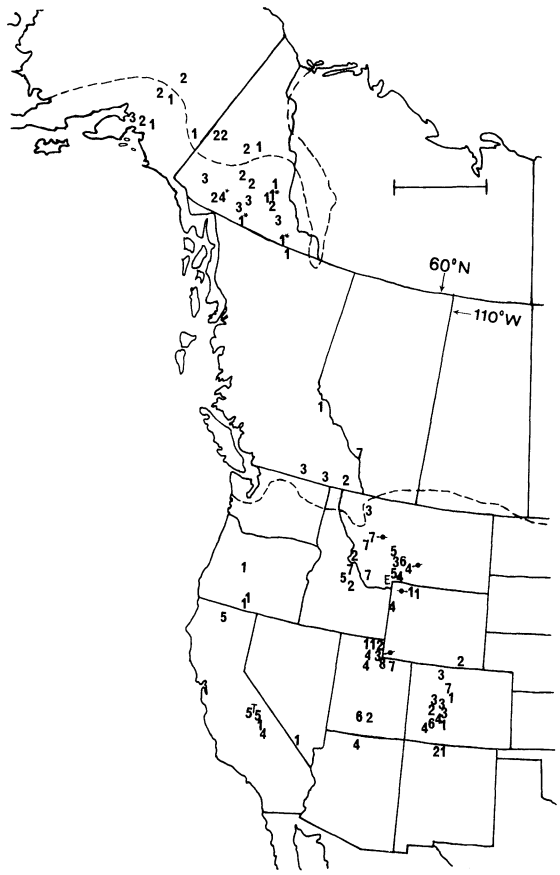

FIG. 1.—Map of western North America showing the geographic distribution of 84 populations of *Antennaria rosea*, combining the results from this study and the previous one (BAYER 1990*b*). Populations from the previous study include all sites south of 60° N and four sites marked with an asterisk north of 60° N. The 21 populations from the current study are all those north of 60° that are not marked with an asterisk. 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 10 and 11 clones are represented by the letters *T* and *E*, respectively. The four populations containing triploids are marked by solid circles with arrow pointing at them, whereas the 80 tetraploid populations are not tagged. The Wisconsinan glacial maxima, based on maps provided in PREST (1984), are marked with dashed lines. For simplicity, the western Canadian ice-free corridor (Alberta) is not shown. Bar = 500 km.

were good predictors of clonal diversity in populations. Kendall's τ_b (SPSS-pc; ZAR 1984; NORUSIS 1988) was calculated to test the relationship between the sexual progenitor number and distance from the center of maximum sexual diversity. 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. Finally, the log likelihood ratio was used to test whether there was a difference in clonal diversity between glaciated and ungla-

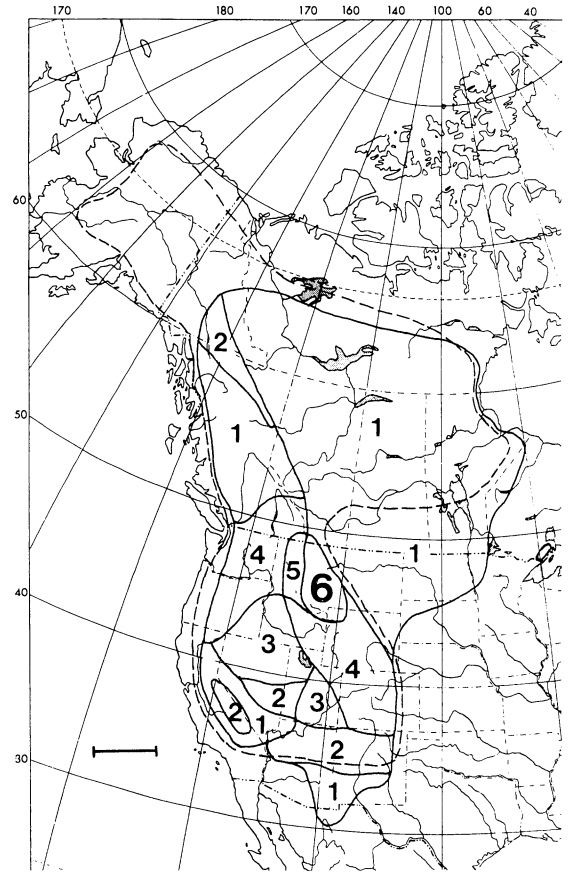

FIG. 2.—Map of western North America illustrating ranges of *Antennaria rosea* and its sexual relatives. The range of *A. rosea* is indicated by a dashed line. The ranges of the sexual species are indicated by solid lines, and numbers inside each region are the sexual diversity indices, which are simply the number of sexual species that are sympatric within each region. Reprinted with permission from Am. J. Bot. (BAYER, R. J. 1990. 77:1314). Bar = 500 km.

ciated regions in the subarctic: Alaska, Yukon, and northern British Columbia.

Results

The geographic distribution of the 21 populations from the current study, the numbers of distinct clones within each, and whether or not that population is from an area that was glaciated or unglaciated during the Wisconsinan appear in figure 1. The geographic distribution of the number of sexual taxa related to and sympatric with *Antennaria rosea* is shown (fig. 2); the geographic distribution of the 84 populations of the expanded study appears in figure 1. The range in distance among populations of the expanded study was 12 to 4,110 km (fig. 1).

In the current study, four alleles for Acp-1, Pgi-3, and Tpi-3 and three at Lap-1 were detected. These values compare with three, six, six, and five for those respective loci in the previous study. Only one new allele (Acp-1^x) was found in the current study. The remainder of the alleles had been encountered previously in *A. rosea* (BAYER 1989*a*, 1990*b*). A total of 37 clones was detected among the 560 individuals from the 21 populations that were observed (table 2). None of the 37 clones was the same as the 192 clones in the previous study (BAYER 1990*b*). The expanded data set, therefore, detected a total of 229 unique clones from 1,623 individuals from 84 populations. Genotypic frequencies of the apomicts from the current study ranged from 0.0036 to 0.0911 ($\bar{X}$ = 0.027 ± 0.022; table 2). Most of the apomicts were very restricted, as 91.9% (34/37) occurred in only one population (fig. 1; table 2). Of the remaining clones, 5.4% and 2.7% occurred in two or three populations, respectively (fig. 1; table 2),

TABLE 2

GENETIC STATISTICS FOR 21 POPULATIONS OF ANTENNARIA ROSEA FROM SUBARCTIC NORTH AMERICA

Clone	ACP	LAP	PGI	TPI	NUM	POPS	FREQ
1....	aabb	bbbb	bddd	bddd	3	1	.0054
2....	aabb	bbbc	bddd	ddee	4	1	.0071
3....	aabb	bbbd	aadd	dddd	5	1	.0089
4....	aabb	bbbd	bddd	cddd	9	1	.0161
5....	aabb	bbbd	bddd	cdde	30	1	.0536
6....	aabb	bbdd	aadd	dddd	10	1	.0179
7....	aabb	bbdd	bddd	bdde	11	1	.0196
8....	abbb	bbbb	bbdd	bddd	25	1	.0446
9....	abbb	bbdd	bbdd	bddd	5	1	.0089
10....	abbb	bbdd	bbdd	bdde	21	1	.0375
11....	abbb	bbdd	dddd	bddd	7	1	.0125
12....	abbb	bccd	bddd	bdde	10	1	.0179
13....	abbc	bbdd	aadd	bddd	23	1	.0411
14....	abbc	bbdd	aadd	cddd	5	1	.0089
15....	abbc	bbdd	bbdd	dddd	20	1	.0357
16....	abbc	bbdd	bddd	bddd	15	1	.0268
17....	abbc	bbdd	bddd	dddd	28	1	.0500
18....	bbbb	bbbb	bbdd	bdde	6	1	.0107
19....	bbbb	bbbb	bbdd	ddde	17	1	.0304
20....	bbbb	bbbb	cddd	ddde	32	1	.0571
21....	bbbb	bbbb	dddd	bddd	16	1	.0286
22....	bbbb	bbbd	dddd	bddd	5	1	.0089
23....	bbbb	bbdd	bbdd	bdde	3	1	.0054
24....	bbbb	bbdd	bddd	bdde	12	1	.0214
25....	bbbc	bbbb	bddd	ddde	47	2	.0839
26....	bbbc	bbbc	bddd	ddde	2	1	.0036
27....	bbbc	ccdd	bddd	bddd	11	1	.0196
28....	bbcc	bbbb	bbdd	cddd	7	1	.0125
29....	bbcc	bbbc	bddd	bdde	21	1	.0375
30....	bbcc	bbbc	bddd	dddd	17	1	.0304
31....	bbcc	bbbd	aadd	cddd	5	1	.0089
32....	bbcc	bbbd	bddd	cdde	51	3	.0911
33....	bbcc	bbdd	aadd	cddd	33	2	.0589
34....	bccc	bbbb	bbdd	bdde	11	1	.0196
35....	bccc	bbbb	bbdd	ddde	4	1	.0071
36....	bccc	bbdd	bbdd	bdde	24	1	.0429
37....	xaab	bbbb	bddd	bddd	5	1	.0089

NOTE.—Thirty-seven unique multilocus genotypes were detected among the populations. Presented are the clone designations (clone), genotype at each of four isozymes (ACP, LAP, PGI, and TPI), total number of each clone detected from all populations (NUM), number of populations in which the clone occurred (POPS), and genotypic frequency (FREQ).

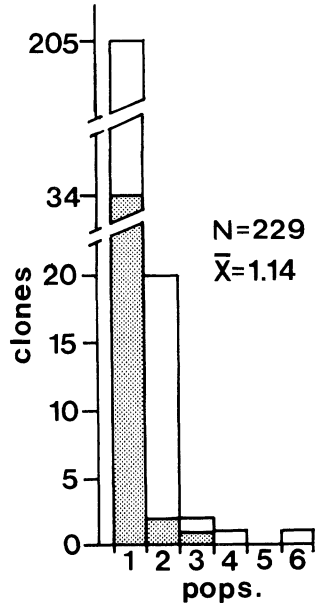

FIG. 3.—Histogram illustrating the frequency distribution of 229 unique multilocus genotypes among 84 populations of *Antennaria rosea* from throughout the range in western North America, representing the combined results of the current study and the previous one (BAYER 1990*b*). Genotypes from the current study are represented by the shaded areas of the histogram, whereas the unshaded areas represent those from the previous study. "Pops." = number of populations in which each unique "clone" was detected. Mean number of populations that each clone occurred in was 1.14.

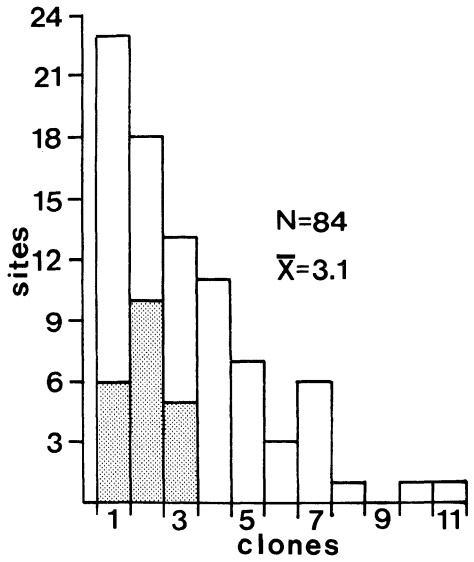

FIG. 4.—Histogram showing the number of clones found in each of 84 populations of *Antennaria rosea* from throughout the range in western North America, representing the combined results of the current study and the previous one (BAYER 1990*b*). Number of clones from the current study is represented by the shaded areas of the histogram, whereas the unshaded areas represent those from the previous study. "Sites" = the actual number of sites containing a given number of "clones." Mean number of clones per population was 3.1.

and the average distance among populations containing the same clone was 432 km (range 207 to 655 km). The average number of populations that each apomict occurred in was 1.11 (fig. 3), comparable to the 1.14 value found in the previous study (BAYER 1990*b*). The expanded study revealed that each of the 229 unique clones was found in an average of 1.135 populations (fig. 3).

A useful indicator of the clonal diversity in *A. rosea,* as it is related to sample size, is the mean proportion distinguishable value, and in the current study it ranged from 0.031 to 0.125 ($\bar{X}$ = 0.076). In the expanded study the mean proportion distinguishable varies from 0.031 to 1.0 ($\bar{X}$ = 0.2088). Populational clonal diversity in the current study varies from one to three multilocus genotypes per population ($\bar{X}$ = 2.0 clones per population; fig. 4). Twenty-nine percent of the populations were monoclonal, whereas 71% were polyclonal (fig. 4). Clonal diversity in the expanded study ranged from one to 11; monoclonal populations were 21% and polyclonal 79% (fig. 4).

Linear regressions showed that in the expanded study, sexual progenitor number (F = 22.92, P < .0001) and distance from the area of maximum sexual diversity (F = 18.22, P = .0001) are highly significant predictors of the number of clones per population. Likewise, elevation (F = 10.71, P = .0016), latitude (F = 11.01, P = .0014), and longitude (F = 11.17, P = .0013) in the expanded study were significant predictors of the number of multilocus genotypes within populations. It should be mentioned that because of the distribution of sites (fig. 1) with respect to latitude and longitude, a correlation of one of these geographic variables with clone number almost certainly assures a correlation with the other. In the previous study (BAYER 1990*b*), latitude, longitude, and elevation were not significant predictors of clonal diversity, but sexual progenitor number and distance from the area of maximum sexual diversity were significant. This indicates that populations of *A. rosea* that are sympatric with one or very few sexual species and are a considerable distance from western Montana (the center of sexual diversity; fig. 2) have lower numbers of clones. Populations that are sympatric with greater numbers of sexual species or are near the center of sexual diversity tend to have higher numbers of apomicts (fig. 2). Also, northern, western, and elevationally high sites tend to have fewer clones per population than southern, eastern, and elevationally low populations. 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 unglaciated (G = 16.6, P < .05; fig. 2). However, the difference is not significant when the comparison is restricted to

populations from glaciated and unglaciated regions of Alaska, Yukon, and northern British Columbia only ($G = 4.2$, $P > .10$).

Discussion

The current study, as the previous one (BAYER 1990*b*), revealed a relatively large amount of clonal diversity in *Antennaria rosea.* Nonetheless, the estimate of diversity is undoubtedly a conservative one, as more clones might have been detected if additional polymorphic loci could have been exploited. ELLSTRAND and ROOSE (1987) and BAYER (1990*b*) have established that the number of clones detected is more a function of loci surveyed than the number of clones assayed per population. Values for most of the population genetic statistics in the current study are equivalent to those from the previous one (BAYER 1990*b*). For example, all of the alleles that are found in the arctic clones, except for one, are also found in populations from the previous study (BAYER 1990*b*). One possible exception is that the number of clones per population in these northern populations ($\bar{X} = 2.0$) is lower than those from the previous study ($\bar{X} = 3.5$), which includes mainly populations from the southern portion of the range of the species. The overall pattern of population structure in *A. rosea* is one in which the majority of the populations are polyclonal, although the average number of clones per population is relatively small ($\bar{X} = 3.1$). In general, clones are restricted to one or two populations ($\bar{X} = 1.14$), and therefore, very few widespread clones exist.

The populations in the subarctic are characterized by relatively low amounts of clonal diversity when compared with those from southern latitudes, the average number of clones being only 2.0 per population. There is a significant negative correlation between latitude and clone number in populations of *A. rosea.* Considering all of the available information on clonal diversity in *A. rosea,* it seems likely that *A. rosea* did not survive the last glacial episode in the northern glacial refugium, Beringia. It is now generally believed that large portions of Beringia in central Alaska and Yukon were covered by grassland or open woodland during the Wisconsinan (MURRAY 1981; MURRAY et al. 1983), and these could have supported populations of *A. rosea.* Therefore, if *A. rosea* did survive in Beringia, then it might be expected that the number of clones per population would be comparable to that found south of the glacial margin in the U.S. Rockies. The historical contention of FERNALD (1925) and HULTÉN (1937) that genetic diversity in refugial survivors is sharply reduced due to harshness of conditions and size reduction in the refugium seems to receive little support from recent empirical data (MURRAY 1981). In fact, several isozyme studies have shown that narrowly restricted endemic species of *Antennaria* display relatively equivalent amounts of genetic diversity when compared to widespread species of the genus (BAYER and CRAWFORD 1986; BAYER 1989*c*). Further support for the phytogeographic hypothesis is supplied by the lack of a significant difference in clonal diversity between glaciated and unglaciated sites in Yukon and Alaska, the stronger line of demarcation in clonal diversity being along the southern glacial margin near the U.S./Canada border. A likely scenario for the phytogeographic pattern of clonal diversity is one that envisions *A. rosea* surviving the Wisconsinan south of the glacial margin or perhaps arising in that region at the end of the Wisconsinan. Migration of the species followed the subsequent recession of the glaciers. The most probable effect that glaciation had on clonal diversity in *A. rosea* would have been to extirpate populations that had become established north of the southern glacial margin prior to the Wisconsinan.

New clones of *A. rosea* are probably generated through the backcrossing of facultatively apomictic clones to their sexual progenitors (BAYER 1990*b*). This is reasonable because the highest amount of clonal diversity is found in populations that occur in areas where the greatest diversity of sexual progenitor taxa exists (BAYER 1990*b*). In areas where populations of *A. rosea* are allopatric from their sexual progenitors, only mutation and migration can contribute to clonal diversity. Additional data from this study continue to support this hypothesis because sexual progenitor number is significantly correlated with clone number per population. The "frozen niche variation" model of VRIJENHOEK (1984) predicts that there should be fewer asexual clones in populations that are sympatric with related sexual species due to displacement of some of the clones as a result of competition with sexual individuals. This study of clonal diversity in *A. rosea* does not seem to uphold this zoologically based model very well, in that populations of *A. rosea* are most diverse clonally when they are sympatric or parapatric with populations of their sexual ancestors. The lack of clonal diversity in the subarctic and arctic could, therefore, be the result of a combination of recent migration and a lack of sexual progenitors in the region. New clones probably cannot arise easily in the north via crossing of facultatively apomictic clones of *A. rosea* to their sexual progenitors, as most of the eight sexual progenitor taxa are absent from the north. Only *A. media* and *A. microphylla* occur in the subarctic and then only in the southern portion of the Yukon.

The possible lack of diversity in geographically marginal but primarily sexually reproducing plant populations has been the subject of several in-

vestigations. PERRY and KNOWLES (1989) discovered that geographically isolated populations of *Acer saccharum* Marsh in Ontario had relatively high amounts of genetic diversity and that no obvious geographic patterns of genetic variation occurred. TREMBLAY and SIMON (1989) also found relatively high amounts of genetic variability in marginal populations of *Picea glauca* (Moench) Voss. On the other hand, LAGERCRANTZ and RYMAN (1990) have demonstrated that genetic variability in *Picea abies* (L.) Karst. was strongly affected by the last glaciation. Those refugial populations having gone through a severe genetic bottleneck due to glaciation were genetically more depauperate than large widespread ancestral populations (LAGERCRANTZ and RYMAN 1990). Both YEH and LAYTON (1979) and FURNIER and ADAMS (1986) found that marginal populations of *Pinus contorta* Dougl. and *Pinus jeffreyi* Grev & Balf., respectively, had less genic variability than geographically central ones. HERMANUTZ et al. (1989) found that localized Baffin Island populations of *Betula glandulosa* Michx. had relatively low amounts of clonal diversity and reproduced primarily by asexual means. Genetic variation in *Sarracenia purpurea* L. is greater in geographically central populations from unglaciated terrain in eastern North America than in northern populations from the glaciated region of eastern North America (SCHWAEGERLE and SCHAAL 1979). INOUE and KAWAHARA (1990) found decreased genetic diversity in insular populations of *Campanula punctata* Lam. as compared with mainland ancestral populations. Genetic diversity tends to decrease with distance of the island from the mainland. In *A. rosea,* northern populations are obviously less diverse than geographically central and southern ones. In the subarctic, *A. rosea* occurs essentially on islands of drier forest openings in a more or less continuous boreal forest, while in the southern Rockies there is much more available habitat for *A. rosea.* The quality and quantity of the available habitats in the north, therefore, may also play a role in inhibiting clonal diversity in *A. rosea.*

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