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EVIDENCE OF PARTIAL APOMIXIS IN *ANTENNARIA MEDIA* (ASTERACEAE: INULEAE) DETECTED BY THE SEGREGATION OF GENETIC MARKERS¹

RANDALL J. BAYER,² KERMIT RITLAND,³
AND BRETT G. PURDY²

²Department of Botany, University of Alberta, Edmonton, Alberta, T6G 2E9; and

³Department of Botany, University of Toronto, Toronto, Ontario, M5S 3B2

ABSTRACT

The interplant variation in sexual and asexual reproduction in an Oregon population of the alpine perennial *Antennaria media* was investigated. Four polymorphic loci were assayed by enzyme electrophoresis of the progeny of 72 families from two subpopulations of *A. media*. The population was divided into two spatially distinct subpopulations. A multilocus model, incorporating a mixture of apomixis and random outcrossing, was used to estimate the mating system of pistillate plants both on the population and individual levels with statistical significance of the estimates based on bootstrap methods. The population contained a mixture of sexual individuals, partial apomicts, and obligate apomicts. The first subpopulation contained individuals that were partially apomictic and presumably produced both reduced and unreduced embryo sacs. There was a conspicuous difference in the breeding system composition between the two subpopulations. The first subpopulation had a "female" biased gender ratio and contained mostly obligate apomicts, some partial apomicts, and some outcrossing amphimicts. The second subpopulation, which had a nearly balanced gender ratio, contained mostly amphimicts, some obligate apomicts, but no facultative apomicts. This is the first study to document partial apomixis in individual plants by the use of genetic markers.

GAMETOPHYTIC apomixis usually evolves in polyploid species within a group and results in the formation of polyploid agamic complexes (Stebbins, 1950; Grant, 1981). Gametophytic apomixis (hereafter referred to as apomixis) within such species complexes results in the formation of an enormous number of asexual clones within the complex (Stebbins, 1950; Grant, 1981). Apomicts have usually been categorized as either obligate or facultative, where individuals produce only unreduced, or both reduced and unreduced, embryo sacs, respectively, on the same plant. Several authors have questioned whether obligately apomictic species exist in nature, because residual sexuality has been found in even those plants that were long thought to be obligate apomicts (Nogler, 1984). If this is true, then it is not justifiable to maintain the two categories (Nogler, 1984); it is more logical to interpret apo-

mictic phenomena as a continuum ranging from complete sexuality through facultative apomixis to nearly obligate apomixis. Species having both amphimictic (sexual) and apomictic (*sensu lato*) individuals have been alluded to in many genera (Nygren, 1954; Fryxell, 1957; Richards, 1970; Harper, 1982; Jenniskens, Den Nijs, and Huizing, 1984).

Within individuals, direct cytological or genetic proof of facultative apomixis has been shown only occasionally. The proportion of amphimixis and apomixis within individual facultative clones is probably genetically determined (Nogler, 1984), but it has been shown that environment also affects the proportions of each reproductive mode within clones. Knox (1967) has shown that environment influences the frequency of apomixis in *Dichanthium aristatum* (Poaceae). Nogler (1984) has pointed out other groups, citing factors including presence of staminate parents, photoperiod, temperature, and chromosome doubling as influencing the degree of apomixis. Unfortunately, studies that investigate the relative frequency of apomixis, facultative apomixis, and sexuality within individual plants in natural populations are lacking.

Antennaria Gaertn. (Asteraceae, Inuleae) is a genus of dioecious plants in which polyploid agamic complexes are common. It has been

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TABLE 1. Gene frequencies^a of the most common alleles in each of the two subpopulations of *A. media*

Locus	Subpopulation	
	A	B
<i>Acp-1</i>	0.93 (0.08)	0.93 (0.03)
<i>Aat-1</i>	0.79 (0.10)	0.98 (0.01)
<i>Lap-1</i>	0.84 (0.06)	0.92 (0.02)
<i>Pgi-3</i>	0.88 (0.06)	0.84 (0.05)

^a Standard errors in parentheses.

shown that pistillate plants from populations of *A. parlinii* Fern., a predominantly hexaploid species from eastern North America containing both staminate and pistillate plants, fail to set seed in isolation (Bayer and Stebbins, 1983). These same plants set abundant seeds when pollinated. Plants from the all-pistillate populations of *A. parlinii* set high percentages of seeds when isolated from staminate plants (Bayer and Stebbins, 1983). A few "female" biased populations were partially apomictic, as they contained both sexual and asexual pistillate plants as well as some staminate plants (Bayer and Stebbins, 1983). Based on this, it has been presumed that the majority of populations containing both staminate and pistillate individuals are fully amphimictic, whereas those containing only pistillate clones are entirely apomictic. However, the actual situation in many populations may not be as simple as we initially envisioned based on these earlier observations and studies. The extent to which amphimixis (sexual reproduction), facultative apomixis, or nearly obligate apomixis exists in either the mixed staminate/pistillate or the all pistillate populations is unknown.

In this paper, we investigate the interplant variation in sexual and asexual reproduction in a mixed staminate and pistillate population of *A. media*, which occurs in alpine habitats throughout western North America. This species is predominantly tetraploid ($2n = 56$), but diploid populations, as well as higher polyploids, are also known (Bayer and Stebbins, 1987). Diploid populations contain approximately equal frequencies of staminate and pistillate plants and are presumably sexual. It is often pointed out that gametophytic apomixis is rare among diploid plants (Asker, 1980; Nogler, 1984), and in most *Antennaria*, including *A. media*, the threshold ploidy level for apomixis is tetraploid (Bayer, 1987). Some tetraploid *A. media* populations contain approximately equal proportions of staminate and pistillate clones, whereas other populations are composed entirely of pistillate clones (Bayer, 1987; R. J. Bayer, personal field observations). Populations with both staminate and pistillate

clones are prevalent in the Sierra Nevada and Cascade mountain ranges, while populations with only pistillate plants are widespread throughout the remainder of the range primarily in the Rocky Mountain cordillera from New Mexico to the Yukon and the northern Cascades in Washington and British Columbia.

MATERIALS AND METHODS—A population of *A. media* from Oregon, near the margin of the range of the populations containing both staminate and pistillate clones, was selected for the purpose of a detailed analysis of interplant variation in sexual and asexual reproduction. For such analyses, the progeny of individual pistillate plants must be considered as arising from some mixture of apomixis or amphimixis. Furthermore, the amphimictic progeny must be outcrossed, since self-fertilization cannot occur in dioecious plants. We use a multilocus model incorporating a mixture of apomixis and random outcrossing to estimate, using isozyme data, the mating system of individual pistillate plants in *A. media*.

The study population is located in Lane Co., Oregon, in the Three Sisters Wilderness, Cascade Range, on the west slope of North Sister, along forest trail #3528 at Obsidian Cliffs, on moist alpine tundra at treeline. The population consists of two spatially distinct subpopulations that have the potential for gene flow between them. The trail traverses the upper subpopulation (hereafter referred to as Obsidian A) at 1,844 m near the top of a small creek drainage that empties into White Branch Creek. About 200 m southwest down the drainage from Obsidian A is Obsidian B at an elevation of 1,832 m. The two subpopulations are separated by a small grove of *Pinus contorta* and *Tsuga mertensiana*. Specimens collected as vouchers to document population variation in morphology are deposited at ALTA as Bayer, Michaels, and Stebbins OR-831 (for Obsidian A) and Bayer, Michaels, and Stebbins OR-832 (for Obsidian B). Both subpopulations contained staminate clones, but Obsidian A was distinctly female biased (gender ratio = 0.07:0.93), whereas Obsidian B had approximately equal numbers of staminate and pistillate plants (gender ratio = 0.46:0.54). Ripe seeds were collected from individual pistillate plants in early September. Forty-one families were collected at random from Obsidian A and 31 from Obsidian B.

Seeds were germinated in growth chambers at 20 C, following a 3-month vernalization period at 4 C. One- to 2-month-old seedlings were used. Progeny were surveyed from each of 72

TABLE 2. Estimates^a of outcrossing rates and gene fixation indices for each subpopulation. Completely apomictic families were excluded from this analysis

Parameter	Subpopulation	
	A	B
Outcrossing rate ^b		
Multilocus outcrossing rate	0.41 (0.17)	0.86 (0.04)
Single locus outcrossing rate	0.46 (0.20)	0.79 (0.04)
Difference	-0.05 (0.07)	0.07 (0.02)
Fixation indices		
Two-gene fixation index	0.12 (0.04)	0.23 (0.02)
Variance of two-gene fixation index	0.05 (0.02)	0.08 (0.02)
Three-gene fixation index	0.03 (0.03)	0.05 (0.03)
Four-gene fixation index	0.02 (0.02)	0.02 (0.01)
No. of families	10	18
No. of progeny over all families	311	268

^a Standard errors in parentheses.

^b Rate of apomixis = 1 - rate of outcrossing.

single plant progeny arrays (range 3 to 35; average 18.6), including 1,339 individual plants. Four polymorphic isozymes were assayed, including acid phosphatase (ACP-1), aspartate aminotransferase (AAT-1), leucine aminopeptidase (LAP-1), and phosphoglucose isomerase (PGI-3).

Electrophoretic techniques were identical to the methods described in Bayer (1988). Ploidy level was determined for the population using the Feulgen staining technique (Bayer, 1984). Because the population is tetraploid, balanced heterozygotes were scored as having two copies of each allele, whereas unbalanced heterozygotes have one and three copies of the respective alleles. The scoring of loci is based on the assumption of tetrasomic inheritance (Bayer, 1989). Locus and allele designation are the same as those given in Bayer (1988).

Following the scoring of gels, a data matrix containing the encoded genotypes of all 1,339 individuals at four loci was assembled (available at the discretion of the first author upon request). These genotypic data were then used to estimate the proportions of apomixis and random outcrossing, using a modification of the computer program "tetrat" (Ritland, in press), which is available from KR upon receipt of a DOS-formatted floppy disk. It uses a multilocus model and the maximum likelihood method to find estimates. Our analyses differ primarily from previous mating estimation studies because they incorporate: 1) apomixis, as opposed to self-fertilization; 2) tetrasomic inheritance, as opposed to disomic inheritance; and 3) the need, because of tetraploidy, to estimate four-gene fixation indices (Ritland, 1987) in order to infer parental genotypes.

The female biased Obsidian A subpopulation was found to contain a considerable num-

ber of families with all identical progeny, indicating complete apomixis. The Obsidian B subpopulation contained fewer such families. Since the objective of this study was to detect mothers with partial apomixis, families with identical progeny (complete apomixis) were excluded from the following analysis. First, the proportion of outcrossing (= 1 - proportion of apomixis) was estimated for each subpopulation. This proportion was estimated first with a multilocus model and then with a single-locus model (with estimates averaged over loci). Second, multilocus estimates of outcrossing were obtained for individual plants, with pollen gene frequency assumed homogenous among plants.

The statistical variance of estimates was determined by the bootstrap method, which creates replicate datasets by sampling observations (with replacement) from the original dataset; the distribution of estimates among these replicate datasets represents the estimation variance. For subpopulation estimates, entire families were resampled. For family (i.e., individual plant) estimates, individual progeny within a family were resampled. Since the distribution of estimates was often skewed for individual plants that were largely apomictic, the empirical distribution of 100 bootstraps was used to find 95% confidence intervals of family estimates.

RESULTS AND DISCUSSION—*Subpopulation outcrossing rates*—Gene frequencies for each subpopulation are given in Table 1. These frequencies are rather extreme but were adequate for mating system estimation. Table 2 gives estimates of outcrossing rates and gene fixation indices for each subpopulation. In both populations, significant proportions of apomixis

TABLE 3. Estimates of outcrossing rate t for individual plants, with genotype of plant and number of progeny N assayed for each plant. Plants with fewer than ten assayed progeny were excluded here

Plant ^a	Genotype ^{b,c}	N	t	95% CI (t) ^{d,e}	
				Lower	Upper
A1	1 1 1 1	32	0.00	a	a
A2	1 1 1 1	20	0.00	a	a
A3	1 1 1 1	24	0.00	a	a
A4	1 2 1 1	31	0.00	a	a
A5	1 2 1 1	32	0.05	non-zero ^f	0.15
A6	3 3 2 2	34	1.00	0.90	1.00
A7	1 2 1 1	33	0.23	non-zero	0.42
A8	1 1 2 1	28	0.84	0.68	0.95
A9	1 2 1 1	20	0.30	non-zero	0.70
A10	1 2 1 1	34	0.09	non-zero	0.23
A11	1 2 1 1	33	0.14	non-zero	0.28
A12	1 2 1 1	32	0.00	a	a
A13	1 2 1 1	33	0.00	a	a
A14	1 2 1 2	33	1.00	0.95	1.00
A15	1 1 1 3	35	0.00	a	a
A16	1 1 1 1	17	0.00	a	a
A17	1 1 1 1	22	0.00	a	a
A18	1 1 2 3	23	0.00	a	a
A19	1 2 2 1	34	0.00	a	a
A20	1 1 2 3	32	0.03	non-zero	0.10
A21	1 1 1 1	12	0.00	a	a
A22	1 1 2 1	21	0.00	a	a
A23	1 1 2 1	10	0.00	a	a
A24	1 1 2 3	32	0.00	a	a
A25	1 2 1 1	32	0.00	a	a
A26	1 1 2 1	22	0.00	a	a
A27	1 1 2 3	19	0.00	a	a
A28	1 3 3 2	32	1.00	0.95	1.00
A60	1 1 1 1	16	0.00	a	a
A61	1 1 1 1	13	0.00	a	a
A62	1 1 1 1	14	0.00	a	a
A63	1 1 1 1	11	0.00	a	a
A64	1 1 1 1	10	0.00	a	a
A65	1 1 1 3	14	0.00	a	a
B29	1 2 3 1	32	0.00	a	a
B30	1 2 1 1	29	0.00	a	a
B31	1 1 1 1	30	0.00	a	a
B32	1 1 1 1	32	0.00	a	a
B33	1 1 1 1	32	0.00	a	a
B34	1 1 3 2	32	0.83	0.63	1.00
B35	1 3 1 1	23	0.75	0.56	0.96
B36	2 1 3 2	22	1.00	0.85	1.00
B37	1 1 3 3	14	0.85	0.75	1.00
B38	1 1 2 1	15	0.73	0.40	1.00
B39	1 1 1 1	13	0.99	0.95	1.00
B40	1 1 1 3	21	0.83	0.61	1.00
B41	1 1 3 1	17	0.68	0.40	0.98
B43	3 1 4 1	18	0.95	0.90	1.00
B44	1 1 3 2	13	0.64	0.36	0.94
B45	1 2 1 1	12	0.49	0.58	1.00
B46	3 1 1 2	19	0.96	0.82	1.00
B50	4 1 1 1	12	0.68	0.43	1.00

^a A = subpopulation A; B = subpopulation B.

^b 1 = AAAA, 2 = AAAa, 3 = AAaa, 4 = Aaaa, 5 = aaaa.

^c Order of multilocus genotypes: *Acp-1*, *Lap-1*, *Aat-1*, and *Pgi-3*.

^d The confidence interval (CI) for t was determined by the empirical distribution of 100 bootstrap estimates.

^e a = apomictic individuals, in which CI cannot be assigned.

are indicated, since outcrossing rates ($= 1 - \text{apomixis rate}$) were significantly less than unity.

However, in subpopulation B, the multilocus outcrossing rate was significantly greater than the single-locus outcrossing rate. This indicates the presence of biparental inbreeding (Shaw and Allard, 1981), and in fact, it is possible that the 14% apomixis estimated with the multilocus model may be entirely due to biparental inbreeding, i.e., it is "apparent apomixis" caused by mating between relatives. This is because multilocus estimates of outcrossing do not exclude all apparent inbreeding (or apomixis) unless a large number of loci, ca. ten, all with "good" gene frequencies (ca. 0.25–0.75) are used (Ritland, unpublished data). By contrast, the estimates for subpopulation A in Table 2 show little evidence for biparental inbreeding: single vs. multilocus estimates of outcrossing do not differ, and the levels of gene fixation are lower. Thus, partial apomixis is probably present in subpopulation A.

Gene fixation indices—The two-gene fixation index, which is the correlation between two alleles sampled at random (without replacement) from the four alleles at a tetraploid locus, was significantly positive in both populations (Table 2). This index is Wright's classical inbreeding coefficient (Wright, 1969) and has an alternative interpretation as the probability that the pair of alleles are identical by descent. The variance of the two-gene fixation index, which measures how much the two-gene fixation index varies among individuals, was also significantly positive (Table 2). By contrast, the three-gene and four-gene fixation indices, which describe the higher-order correlations between triplets and quadruplets of alleles (Ritland, 1987), did not significantly differ from zero (Table 2).

The gene-fixation indices provide additional evidence for the pattern of mating practiced in each subpopulation. If plants practice only a mixture of random outcrossing and apomixis, then the fixation indices should all be zero. If plants practice some selfing, all fixation indices should be positive. If localized mating is causing some biparental inbreeding to occur, the

^f An exact lower bounds cannot be estimated because those samples that consisted of all identical (selfed) progeny are not representative of the parent distribution. Since we know the parent distribution must contain outcrossing because of their presence in the original data we can at least conclude the lower bounds is not zero.

lower-order indices should be more positive than the higher-order indices (although by how much is not known). Table 3 seems to indicate the last scenario (biparental inbreeding) holds for these subpopulations, particularly subpopulation B, in which a significant difference between single vs. multilocus estimates of outcrossing also indicated biparental inbreeding.

Individual plant outcrossing rates—The estimates of outcrossing for individual plants are given in Table 3, with 95% confidence intervals. Plants that produced all identical progeny (apomictic plants) are included in these individual estimates, and likewise they all have estimates of 0% outcrossing. However, a confidence interval for the true proportion of apomixis (or outcrossing) could not be determined for these plants, as bootstrap samples also draw identical progeny arrays.

In subpopulation A, six plants (A6, A7, A9, A10, A11, and A20) showed partial apomixis; the confidence interval for t was greater than zero but less than one (Table 3). Five of six plants showed predominant apomixis. By contrast, subpopulation B had only three plants with partial apomixis (B35, B41, and B44), and furthermore, these were predominantly outcrossing. It is possible, since the variance of the two-gene fixation index was strongly positive in subpopulation B (Table 2), that these three plants in this subpopulation practiced excessive biparental inbreeding and did not produce any apomictic progeny. Thus, the presence of partially apomictic plants can be definitely confirmed only in subpopulation A. It is difficult to detect low levels of partial apomixis in a plant because of the possibility of biparental inbreeding causing low levels of "apparent" apomixis.

This is the first study that has determined the statistical significance of outcrossing estimates for individual plants. For this the bootstrap method was applied, where the unit of resampling was individuals within a family (derived from the same plant). Table 3 shows that the statistical error of these individual mating system estimates can be large, and that generally, homozygous genotypes give more reliable estimates. It is recommended that for reliable individual-plant estimates, workers use at least 32, if not 64, progeny assayed at several isozyme loci.

Population structure—Several conclusions can be drawn with regard to the population structure of the Obsidian population of *A. media*. The most striking feature revealed by the study is that this population of *A. media* is

composed of complex mixtures of individuals that have very different modes of reproduction ranging from sexual outcrossers to apomicts. Also noteworthy is the conspicuous difference in the breeding system composition between subpopulation A and subpopulation B, especially considering the 12-m elevational difference over the 200 m that separate them. It is interesting that populations like subpopulation B, which have nearly balanced gender ratios and are presumably completely sexual based on this, can be mixtures of sexual and apomictic individuals. Populations like subpopulation A that are heavily female biased can be mixtures of obligate apomicts, partial apomicts, and amphimicts. The sexual plants themselves can practice a mixture of random outcrossing and biparental inbreeding.

Some of the individuals in subpopulation A are facultatively apomictic and presumably produced both reduced and unreduced embryo sacs. The role played by partially apomictic individuals and/or populations was first elucidated by Clausen (1954) and later supported by Harper (1982). In partially apomictic populations, variant apomictic clones are derived sexually from facultative apomicts and are genetically stable because these plants inherit genes for apomixis (Clausen, 1954; Bayer, 1987). Consequently, facultative apomicts perhaps play the important function of introducing new apomictic clones into populations.

Although mixed populations of sexual and apomictic *Antennaria* have been reported before for *A. parlinii* (Bayer and Stebbins, 1983) and *A. parvifolia* Nutt. (Bierzychudek, 1987), the documentation of the different modes relied on seed set of capitula retained in isolation. This method is less direct than using genetic markers and has several inherent troubles including difficult and perhaps subjective scoring of viable and inviable achenes. Also, the isolation bags themselves create artificial conditions that can cause abortion of some or all asexual-produced ovules in a head, thereby giving the false impression that the isolated plant is sexual. Individuals that produce a few seeds in isolation are disconcerting because they could be obligate apomicts that have aborted some seeds, facultative apomicts, or sexuals that have secured pollination by stray pollen entering a faulty isolation bag. It is very difficult to detect partial apomixis using such a system. By exploiting genetic markers we were able to better document the occurrence of facultative apomixis. Additionally, we were able to establish the relative proportions of the different reproductive modes within the population.

Evolutionary implications—Bierzychudek's review of plant parthenogenesis (1985) has pointed out that apomictic species often occur in more extreme environments, such as high elevations or more northerly latitudes than their sexual counterparts. This correlate seems to hold for presumed predominantly sexual and apomictic populations of *A. media*. The reasons for these distributions are unclear, but she has suggested that in *Antennaria* it may be due to the selective forces of infrequent or unreliable pollinators in severe habitats (Bierzychudek, 1987). The Obsidian population occurs on the margin of the range between populations containing approximately equal numbers of staminate and pistillate plants and those composed entirely of pistillate individuals. Our study of this dynamic population points to the fact that the reproductive structure of populations of *Antennaria* may not be as simple as once believed. Perhaps under certain conditions partially apomictic populations like Obsidian have the advantage over fully sexual or apomictic populations in being able to change the relative proportions of sexual and asexual individuals as selection acts to change their relative advantages. It would be interesting to survey pistillate plants from populations with balanced gender ratios, well within the confines of the range of such populations and undoubtedly under different selective pressures. Would populations such as these also contain mixtures of different reproductive modes like the Obsidian population?

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