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DISTRIBUTION OF SEXUAL AND APOMICTIC POPULATIONS OF *ANTENNARIA PARLINII*

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The evolution and adaptive value of sexual reproduction have been the subject of extensive theoretical exploration (Williams, 1975; Maynard Smith, 1978). The major problem centers about the "cost of meiosis," as Williams expresses it. If both sexual and asexual means of reproduction are available to an individual well adapted to its environment, why should it break up its complex adaptive system of genes by segregation at meiosis, on the chance that equally adaptive complexes will be reconstituted by fertilization?

Any empirical answer to this question will require comparisons of related populations that reproduce sexually and/or asexually. The presence over a long period of time of both sexuality and asexuality in closely related populations would indicate that both modes of reproduction are equally adaptive. If reproductive mode varies with geography or ecological conditions, sexuality can be assumed to confer an adaptive advantage under some conditions and asexuality under others, or else the change in relative proportions of the two systems occurs over very long periods of time.

Dioecious, agamospermous species of plants may be useful for testing hypotheses about sexuality because apomictic females will produce only female offspring. Consequently, the sex ratio within a population is a valuable though not an infallible clue to the incidence of asexuality.

Both sexual dioecism and agamic seed production exist in *Antennaria* (Asteraceae, Inuleae), a genus of perennial herbs found in cool temperate to arctic regions

of the northern hemisphere. Taxonomists investigating North American *Antennaria* during the 1880's and 1890's observed that many widespread species consist of populations containing only pistillate plants. The presence of apomixis via diplospory (Gustafsson, 1944; Stebbins, 1950) was determined for species of eastern North America by Stebbins (1932). We believe that three entities recognized by Fernald (1945), namely *A. fallax* Greene, *A. parlinii* Fern., and *A. munda* Fern., should be combined into a single variable species, *A. parlinii* s.l. (Bayer and Stebbins, in press). *Antennaria parlinii* is chiefly hexaploid ($2n = 84$), but includes a few tetraploid ($2n = 56$) and octoploid ($2n = 112$) populations (Bayer and Stebbins, 1981).

Populations of *A. parlinii* may consist entirely of pistillate plants in addition to others in which staminate plants occur (Fernald, 1936). Herbarium specimens from Ohio at The Ohio State University show that staminate plants have been much more commonly collected in the southeastern (unglaciaded) as opposed to the northwestern (glaciaded) part of Ohio. Consequently, this state appeared to be particularly favorable for comparing sexual, apomictic and mixed populations of *A. parlinii*. We have determined that the great majority of both kinds of populations have the same chromosome number, $2n = 84$. The objectives of the present study are to describe the distribution of apomictic and sexual populations in Ohio and their correlation with the glacial history, to document the nature of facultatively apomictic populations in the glacial

TABLE 1. Geographic origin, number of clones examined, frequency of staminate clones, and voucher number for populations of *Antennaria parlinii*. Populations 1-22 are from the unglaciated region, 23-24 are from the glacial margin, and 25-64 are from the glaciated region. Voucher specimens are on deposit at OS. * "undetermined". In these cases the absence of staminate clones was determined by a visual scan in the field, without counting numbers of clones.

County, state	Total number of clones examined	Frequency of staminate clones	Voucher number	County, state	Total number of clones examined	Frequency of staminate clones	Voucher number
1) Athens, Ohio	60	0.533	OU-123	33) Delaware, Ohio	31	0.000	SU-153
2) Athens, Ohio	49	0.693	SH-127	34) Delaware, Ohio	100	0.400	DE-154
3) Belmont, Ohio	11	0.545	BN-132	35) Erie, Ohio	90	0.478	AH-151
4) Belmont, Ohio	undetermined*	0.500	BE-133	36) Fairfield, Ohio	100	0.470	HA-145
5) Coshocton, Ohio	101	0.762	COS-17	37) Fairfield, Ohio	100	0.430	MT-146
6) Guernsey, Ohio	30	0.233	WS-131	38) Fairfield, Ohio	9	0.667	LA-69
7) Guernsey, Ohio	100	0.480	WS-131	39) Fairfield, Ohio	100	0.010	LI-129
8) Harrison, Ohio	73	0.452	NA-134	40) Franklin, Ohio	100	0.580	RS-128
9) Hocking, Ohio	105	0.495	AC-27	41) Franklin, Ohio	97	0.670	DA-1-12
10) Hocking, Ohio	100	0.460	HG-83	42) Knox, Ohio	34	0.412	MV-16
11) Hocking/Fairfield, Ohio	10	0.100	CP-130	43) Knox, Ohio	100	0.000	UT-155
12) Jefferson, Ohio	100	0.540	BZ-135	44) Licking, Ohio	100	0.110	WT-156
13) Monroe, Ohio	47	0.702	LV-121	45) Licking, Ohio	29	0.000	NW-157
14) Monroe, Ohio	11	0.727	LA-122	46) Logan, Ohio	24	0.542	WL-70
15) Noble, Ohio	59	0.305	SL-64	47) Lorain, Ohio	24	0.000	OB-148
16) Perry, Ohio	100	0.680	MX-68	48) Lorain, Ohio	73	0.438	EY-149
17) Tuscarawas/Stark, Ohio	undetermined*	0.000	5063	49) Lorain, Ohio	82	0.000	BH-150
18) Vinton, Ohio	100	0.540	VI-24	50) Mahoning, Ohio	65	0.523	EW-137
19) Vinton, Ohio	102	0.578	NP-29	51) Morrow, Ohio	16	0.000	MO-138
20) Washington, Ohio	94	0.585	WH-126	52) Morrow, Ohio	11	0.000	MR-139
21) Monongalia, West Virginia	34	0.765	MO-124	53) Morrow, Ohio	34	0.000	MG-144
22) Doddridge, West Virginia	100	0.670	DO-125	54) Paulding, Ohio	52	0.000	PD-73
23) Fairfield, Ohio	100	0.320	BK-88	55) Perry, Ohio	13	0.231	PE-66
24) Knox, Ohio	87	0.506	KX-18	56) Richland, Ohio	70	0.000	RI-140
25) Allen, Ohio	89	0.000	LI-72	57) Richland, Ohio	21	0.000	PY-152
26) Ashland, Ohio	100	0.560	MN-141	58) Seneca, Ohio	9	0.000	SE-143
27) Ashland, Ohio	47	0.000	AS-142	59) Stark, Ohio	undetermined*	0.000	5061
28) Auglaize, Ohio	100	0.000	FA-71	60) Stark, Ohio	undetermined*	0.000	5062
29) Columbiana, Ohio	100	0.500	TG-136	61) Williams, Ohio	56	0.000	WI-75
30) Defiance, Ohio	30	0.233	PD-74	62) Wood, Ohio	55	0.000	BE-76
31) Delaware, Ohio	98	0.653	ALC-53	63) Wyandot, Ohio	100	0.000	TH-77
32) Delaware, Ohio	100	0.000	KI-54	64) Wyandot, Ohio	undetermined*	0.000	WY-120

TABLE 2. Percent seed set in *Antennaria parlinii* resulting from either isolation of pistillate capitula or from pollination. The geographic origin and collection number are given for each population from which the pistillate parent originated. — = outcrossed seed set not determined; *U = unglaciated region; G = glaciated region.

Ohio County (location of female)	Collection number of female	Frequency of staminate clones	% seed set in isolation	% seed set with pollination
Coshocton (U)*	COS-17	0.762	0	—
Hocking (U)	AC-27	0.495	0	61
Hocking (U)	HO-67	0.503	0	77
Noble (U)	SL-64	0.305	16	81
Vinton (U)	VI-24	0.540	0	99
Vinton (U)	NP-29	0.578	21	90
Fairfield (U-G)	BK-88-16	0.320	0	100
Fairfield (U-G)	BK-88-03	0.320	9	76
Fairfield (U-G)	BK-88-06	0.320	60	—
Fairfield (U-G)	BK-88-04	0.320	85	100
Fairfield (U-G)	BK-88-17	0.320	65	100
Fairfield (U-G)	BK-88-20	0.320	86	—
Fairfield (U-G)	BK-88-02	0.320	100	—
Fairfield (U-G)	BK-88-05	0.320	98	—
Fairfield (U-G)	BK-88-07	0.320	97	—
Fairfield (U-G)	BK-88-14	0.320	100	—
Knox (U-G)	KX-18-04	0.506	0	98
Knox (U-G)	KX-18-15	0.506	0	78
Knox (U-G)	KX-18-01	0.506	11	—
Knox (U-G)	KX-18-02	0.506	15	95
Knox (U-G)	KX-18-03	0.506	100	—
Knox (U-G)	KX-18-10	0.506	97	—
Knox (U-G)	KX-18-13	0.506	100	—
Knox (U-G)	KX-18-05	0.506	98	—
Knox (U-G)	KX-18-06	0.506	98	—
Knox (U-G)	KX-18-18	0.506	89	—
Knox (U-G)	KX-18-08	0.506	99	—
Auglaize (G)	FA-71	0.000	98	—
Delaware (G)	KI-54	0.000	95	98
Franklin (G)	DA-12	0.670	0	82
Knox (G)	MVE-16	0.412	0	91
Perry (G)	PE-66	0.231	9	82

interface region, and to verify the correlation between sex ratio and sexuality of the population.

MATERIALS AND METHODS

Sex ratios were determined in the field in different regions of Ohio and some adjacent states. Numerous populations were surveyed at the interface of the glaciated and unglaciated regions. We attempted to score the sex of one hundred clones in each population, but populations were not always sufficiently large. The sample of clones was taken along a linear transect through the population. In cases where clones merged, two meters were allowed

between individuals scored, but in most cases individual clones were morphologically and/or spatially distinct and easily distinguished. In many small populations every individual was scored. Plants were obtained from several populations throughout Ohio for isolation experiments in the greenhouse. Clones to be used in isolation experiments were potted in a well drained soil mix and kept in a cool greenhouse, where isolation and crossing experiments were performed in the springs of 1979 and 1980.

Pistillate inflorescences were covered with small bags made from KimWipes that were secured at the bottom with string.

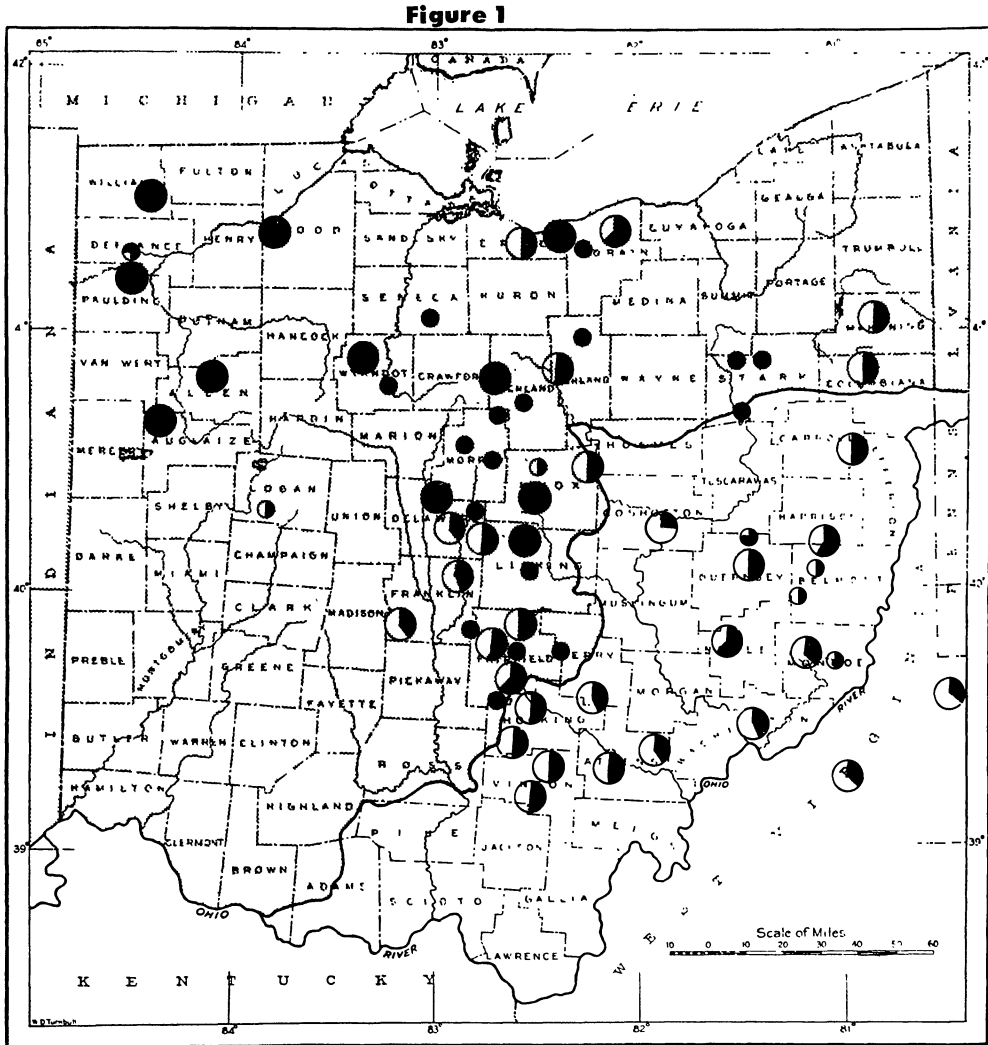


FIG. 1. Proportion of pistillate (dark section of circles) and staminate (light) clones in populations of *Antennaria* in Ohio. Stippled area of the map shows the maximum limits of the glaciated region. Large circles indicate populations in which more than 50 individuals were scored as to sex, small ones less than 50.

Sexual females never set seed under these conditions (Table 2). Control pollinations were made by uncovering an isolated, receptive, pistillate inflorescence and rubbing it with a staminate inflorescence from the same or a similar population. The pollination bags were then replaced. When the fruits were ripe the whole inflorescence was harvested, and a single capitulum was selected to determine the percent seed set.

Contingency tables (Ott, 1977) and bi-

variate plots (SAS Institute, 1979) were employed to determine if the distribution of sexual and asexual populations is due to clinal variation or whether there are two distinct groups correlated with the glacial history of the area.

RESULTS

In Table 1, frequency of staminate plants is reported for populations located in the unglaciated and glaciated regions

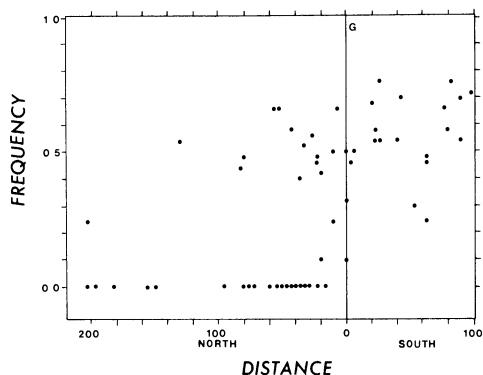


FIG. 2. Frequency of staminate clones of *Antennaria parlinii* with respect to distance from the glacial margin (line G). Frequency of staminate clones is represented along the Y axis while distance north or south of the glacial margin (in kilometers) is presented along the X axis. Five populations in which the total number of clones was not determined (see Table 1) were not considered in this analysis. The frequency of staminate clones in the asexual populations is zero.

and the glacial margin of Ohio, plus two populations from unglaciated West Virginia. These same populations are mapped in Figure 1. Populations having sex ratios that approximate 0.5 staminate or that have a slight excess of staminate plants predominate in the unglaciated region (Fig. 1). On the other hand, most populations listed in Table 2 coming from glaciated regions of northwestern Ohio either lack staminate plants, or have an excess of pistillate plants.

The results of tests in the greenhouse made to determine whether or not sex ratios are a good indicator of the presence and frequency of asexual (agamospermous) seed production are presented in Table 2. With two exceptions (NP-29 and SL-64) clones derived from populations having sex ratios consisting of 0.5 or more staminate plants failed to set seed upon isolation, but set abundant seed after artificial pollination. By contrast, clones derived from all-pistillate populations consistently produced high percentages of seed even when unpollinated. Clones derived from populations that contained staminate

TABLE 3. Relation between glacial history and sexual composition of populations of *Antennaria parlinii*. Five populations in which the total number of clones was not determined and two populations (KX-18 and BK-88) which occur at the glacial margin were not considered in this analysis.

	Number of populations with no staminate clones (asexual populations)	Number of populations with some staminate clones (sexual populations)
Glaciated region	19	18
Unglaciated region	0	20

but had an excess of pistillate plants responded in different ways. As is evident, particularly for those obtained from Fairfield County (BK-88), a single population can include some clones that are strictly sexual, others that are obligate apomicts, and some that are facultative apomicts. Facultative apomixis, which is well known in other genera of angiosperms (Stebbins, 1950), is here reported in *Antennaria* for the first time.

Glaciated areas of Ohio have an excess of apomictic populations, and the shift in sex ratios from southeast to northwest appears to show an abrupt change associated with the terminal moraine. A plot of the proportion of staminate clones against distance from glacial margin (Fig. 2) suggests that the frequency of staminate clones is not clinal, but a step function coinciding with the terminal margin (Fig. 2, line G) of the Wisconsin glaciation. There is a significant association (Table 3) between glaciation and the absence of staminate clones ($\chi^2 = 15.41, P < .001$).

DISCUSSION

Although phenotypic sex reversal is known in angiosperms (McArthur, 1977; Hibbs and Fischer, 1979), the gender of all of the clones of *Antennaria* that we have maintained in culture have remained stable. Among the thousands of clones from several species of *Antennaria* examined in the field, none has been found in which gender differed absolutely or even

proportionately from one flowering stalk or in one capitulum to another in the same clone. Non-genetic variation in gender is very rare or absent.

Apomictic populations of *A. parlinii* in Ohio occur chiefly in glaciated regions, but outside of Ohio apomictic populations occur rather frequently in unglaciated areas (Stebbins, 1932; pers. observ.). In those parts of eastern North America that were covered by the Wisconsin ice sheet, from Minnesota east to Wisconsin, Ontario, New York and New England, staminate clones are generally much less frequent than pistillate clones.

The association between glaciated regions and apomictic populations does not mean that conditions brought about by glaciation are necessary for the spread of apomictic populations of *A. parlinii* although they probably were favorable to it. A consideration of ecological differences between neighboring glaciated and unglaciated areas provides some insight into underlying causes of the association.

Antennaria parlinii is more common southeast of the terminal moraine than northwest of it, no doubt because *A. parlinii* is almost entirely confined to dry oak woodlands dominated by such species as *Quercus alba*, *Q. stellata*, *Q. muhlenbergii*, *Q. borealis maxima*, and *Q. velutina*. These plant communities are much more common in southeastern than in northwestern Ohio. In the northwest, the well drained soil that supports them is confined to gravelly fluvioglacial deposits and rocky margins of some of the river valleys. These favorable sites mark the readvances of the ice sheet during the period of retreat of the ice margin (Flint, 1957). Moreover, the topographic diversity of southeastern Ohio results in a greater diversity of oak woodlands that differ in exposure and drainage.

We believe that where suitable habitats are numerous, close together, and diverse, sexually reproducing females are probably favored. Where such habitats are few, far apart and more similar to each other, females that produce seed asexually are perhaps favored. Apomictic genotypes can

successfully colonize remote habitats and increase rapidly if the habitats are homogeneous. Colonization of such sites by sexual genotypes is less successful because multiple colonization by both females and males is necessary. In contrast, where habitats are abundant but diverse, each is easily colonized by both sexes, and the diversity of habitat types favors production of genetically diverse offspring. Thus some apomictic genotypes may have been preadapted for colonizing new areas and extending the range of the species. As this hypothesis predicts, many populations of a mixed nature occur in central Ohio, along the margins of the region that contains predominantly sexual populations. Facultatively apomictic clones, via fertilization of eggs having genes for apomixis, could give rise to a diverse array of apomictic descendants, as has been shown to be true in *Poa* (Clausen, 1954) and *Potentilla* (Rutishauser et al., 1969). These mixed populations could, therefore, provide a rich source of highly adaptive apomictic clones. We believe that the apomictic complex of *A. parlinii* is young, since in spite of the obvious trend toward widespread fully apomictic populations, sexual populations and facultative apomicts still exist and are locally or regionally abundant (Grant, 1981). This contrasts with the apomictic complexes of *A. rosea* and *A. neodioica* s.l. where no sexual populations are known (pers. observ.; Bayer and Stebbins, in press).

SUMMARY

Populations of the dioecious composite *Antennaria parlinii* along a transect from West Virginia to northwestern Ohio are mostly sexual in the unglaciated southeastern region. In the glaciated region in northwestern Ohio, populations consist entirely or chiefly of pistillate clones. Near the terminal moraine of the Wisconsin glaciation, two populations contain a mixture of sexual, fully apomictic and facultatively apomictic clones. In general, where populations are closely spaced in varied habitats, sexual clones are most successful.

Widely spaced populations are primarily or entirely apomictic, perhaps because of the colonizing ability of the apomicts. The presence of facultative apomicts suggests gradual evolution of obligate apomixis.

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