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ENVIRONMENTAL SENSITIVITY OF SEXUAL AND APOMICTIC *ANTENNARIA*: DO APOMICTS HAVE GENERAL-PURPOSE GENOTYPES?

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Abstract.—The fact that apomictic taxa typically occupy a wider range of environments than their sexual relatives has generated the hypothesis that apomicts are more likely to possess “general-purpose genotypes,” i.e., genotypes whose performance is relatively insensitive to changes in environmental conditions. This hypothesis was tested by cloning sexual and apomictic females of *Antennaria parvifolia* (Asteraceae) and growing each genotype in six growth-chamber environments varying in temperature and moisture levels. A joint regression analysis revealed that the survival of apomictic genotypes was significantly less sensitive to environmental conditions than that of sexual genotypes but demonstrated no differences with regard to flowering or biomass. However, the coefficient of variation in biomass across the six environments was significantly lower for apomicts than for sexuals, and the geometric mean of survival over the six environments was significantly higher for apomicts. Apomicts significantly exceeded sexuals in mean survival, mean flower-head production, and mean biomass. These results support the hypothesis that apomictic genotypes are more “general-purpose” than sexuals, and increase the difficulty of explaining the persistence of sexual reproduction in *A. parvifolia*.

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Recent interest in the evolution of sexual reproduction has led to the rediscovery of a pattern originally identified by Vandell (1928, 1940) and termed by him “geographical parthenogenesis”—the occupancy by asexual taxa of geographical ranges that are different from the ranges of their sexual relatives. The ranges of asexual taxa tend to be larger and to extend to higher elevations and higher latitudes than do the ranges of closely related sexual taxa. Some asexual groups tend to be found in areas that are more arid, more disturbed, or more island-like than the areas occupied by their sexual relatives. In general, asexuals seem more likely than sexuals to occupy marginal or peripheral habitats (Glesener and Tilman, 1978; Bell, 1982; Bierzychudek, 1985).

These patterns have been used to support the contention that sexual reproduction is maintained by “biotic selective forces” (e.g., predation, competition, parasitism), which are thought to be stronger and more prevalent in the central part of a species’ range than in its periphery (Levin, 1975; Glesener and Tilman, 1978; Bell, 1982). Such reasoning has been based on the assumption that asexual and sexual genotypes are fundamentally similar in their ecological properties and that the real advantage of sex-

uality lies in its ability to generate offspring that are genetically diverse rather than genetically uniform. Being part of a brood of genetically diverse individuals is thought to provide sexually produced progeny with some measure of protection against these frequency-dependent selective forces.

However, there are several reasons for expecting that asexual and sexual genotypes are *not* ecologically similar and that asexual genotypes are, in fact, likely to be less sensitive to environmental variability than are sexual genotypes. The first is that many asexual genotypes arise through hybridization followed by polyploidy (Stebbins, 1950) and are thus likely to be more heterozygous than either sexual parent. These hybrids might have the physiological capabilities of both parental lines (Clausen et al., 1945, 1947) and may, in fact, have ecological tolerances that exceed those of either parent (Levin, 1983). Secondly, the absence of recombination in asexual lines creates a fundamental difference in how selection operates on asexual and sexual lineages. In sexual genotypes, where coadapted gene complexes can be broken up by recombination, a broadly adapted parent will not necessarily produce broadly adapted offspring. By contrast, selection on asexual genotypes op-

erates on their composite properties, because it is the entire clone that either goes extinct or is preserved from one generation to the next (Templeton, 1982). An asexual parent that acquires a genotype conferring broad tolerance, either by hybridization or by mutation, will transmit that genotype undisrupted to all of its offspring. Asexual clones that have survived over a number of generations have done so only by virtue of being able to tolerate all of the environmental variation to which they have been subject since their origin. Narrowly adapted asexual clones will certainly arise, but they will go extinct relatively quickly (Templeton, 1982). Finally, if much of the mating by sexual individuals takes place between relatives, sexual individuals may experience some level of inbreeding depression relative to asexuals.

Thus, there are good reasons to expect that asexual genotypes might be better adapted to extreme environments than are sexual genotypes, i.e., that they might better represent "general-purpose genotypes" (a term coined by Baker [1965] in a rather different context). At present, however, there is no experimental evidence that general-purpose genotypes actually exist; what support there is for this hypothesis is circumstantial, derived from descriptive studies, and subject to confounding factors and multiple interpretations (Lynch, 1984).

I report here an experimental comparison of the environmental sensitivity of closely related sexual and asexual genotypes. Sexual and apomictic females of *Antennaria parvifolia* (Asteraceae), a perennial plant of alpine and subalpine habitats, were cloned and grown in a series of growth-chamber environments, and the performance (survival, growth, and reproduction over one growing season) of each genotype across this range of conditions was examined. Using data from this experiment, I attempt to answer the question: do apomictic genotypes display less environmental sensitivity than sexual genotypes?

MATERIALS AND METHODS

The Experimental System

Antennaria parvifolia is a dioecious perennial herb that grows in both alpine mead-

ows and subalpine meadows and forests, as well as at lower elevations. Its range includes much of western North America, extending from the northern borders of Alberta and Saskatchewan to southern Arizona and New Mexico and east from central Nevada nearly to the Missouri River (Bayer and Stebbins, 1987). *A. parvifolia* has a polymorphic breeding system: some females are sexual (and, because they are dioecious, obligately outcrossed), while others are obligately apomictic. Apomixis in *Antennaria* is ameiotic (Stebbins, 1932), and so the progeny of apomictic females are normally genetically identical to one another and to their mothers. The two types of females are morphologically indistinguishable. In contrast to most pairs of sexual/asexual taxa, in which the sexual form is diploid while the asexual form is polyploid (Bierzychudek, 1985), both sexual and apomictic *A. parvifolia* females are highly polyploid, ranging from octoploid to decaploid (Bayer and Stebbins, 1987). Both apomicts and sexual plants are readily propagated vegetatively.

The phenomenon of geographical parthenogenesis is characteristic of *A. parvifolia*, even on a fairly local geographic scale. Populations north of the Canadian border are exclusively apomictic (Bayer and Stebbins, 1987). In central Colorado, populations at and below 2,750 m are either mixtures of sexual and apomictic individuals or else consist solely of sexual males and females. Sexual individuals are uncommon above 2,750 m, however, and are quite rare above 3,100 m. By contrast, apomictic populations are common even as high as 3,500 m (Bierzychudek, unpubl.).

Plants were collected from the Sawatch and West Elk Mountains in central Colorado in early September; only females were used. Plants were judged to be apomictic if seed set occurred in flower heads that were protected from pollen transfer by dialysis tubing (for details, see Bierzychudek [1987]). A variety of sites was sampled to assure that a diversity of apomictic genotypes was represented, and morphological characters were used to establish that the different apomictic individuals differed genetically. All sites were within 80 km of one another; elevations ranged from 2,575 to 3,350 m. Nearly

all sites yielded both sexual and apomictic individuals, including the highest-elevation site (where a single rare sexual female was found). Although 25 sexual genotypes and 24 apomictic genotypes were originally collected, mortality during transit and transplanting reduced these numbers to 11 sexual genotypes and 14 apomictic ones. The difference in survivorship between sexual (44%) and apomictic (58%) genotypes is not significant ($X^2 = 1.06$, $d.f. = 1$, $P > 0.10$). Mortality during transit was also independent of the elevation of the collection site; 49% of the genotypes collected below 3,000 m survived, compared to 50% of those collected above 3,000 m ($X^2 = 0.002$, $d.f. = 1$, $P > 0.95$).

Plants were taken to the Duke University Phytotron, where they were potted in a mixture of sand, gravel, and Turface® and placed in environmental chambers with 8L:16D photoperiods, 20°C days and 10°C nights. Plants were watered daily and fertilized weekly with half-strength Hoagland's solution. After growing under these conditions for three months, the fibrous root system of each genotype was divided into as many equal-sized replicates as possible. Depending on the genotype and its vigor, numbers of replicates varied from four to 60. The initial sizes (area of clones in cm²) of these replicates were measured, and sexual and apomictic genotypes did not differ in mean replicate size (Student's *t* test, $t = 1.75$, $N = 24$, $P = 0.10$).

Each genotype's replicates were evenly distributed among six environmental chambers representing all pairwise combinations of three temperature regimes and two moisture regimes. When replicates were not present in even multiples of six, extras were assigned to chambers at random. The chambers formed a split-plot design with two replicates, with temperatures as main plots and moistures as subplots (i.e., each temperature × moisture combination was represented in each of two chambers). Genotypes were randomized, and their positions were rotated monthly. To represent summer growth conditions, the photoperiod during the experiment was 15L:9D of daylight, with a 14-hour thermoperiod. The three temperature regimes were hot (24°C days, 16°C nights), medium (18°C days, 10°C

nights), and cold (12°C days, 4°C nights); the two extremes represented limits higher and lower than those encountered by plants at low and high elevations, respectively (United States Department of Commerce, 1970–1980). The two moisture regimes were created by watering once daily (wet) or once weekly (dry). In nature, these plants experience a wide range of moisture conditions, from near-drought to near-saturation (Bierzychudek, unpubl.). Nutrients (half-strength Hoagland's solution) were applied once weekly to all plants, regardless of treatment. Plants were placed in these experimental conditions in early February and allowed to grow until July. At this point, the existence of consistent phenotypic differences among the different apomictic accessions with respect to leaf color, shape, growth form, and flower color confirmed that they were indeed distinct genotypes. All plants were censused weekly for mortality, and seed heads were harvested as they matured. After harvest, all plants were dried and weighed.

Data Analysis

I analyzed three measures of performance. The first, "survival," is each genotype's environment-specific probability of living until the experiment was terminated. The second, "flowering," is the mean number of flower heads produced in each environment by individuals that survived. Because these measures are not necessarily well-correlated with lifetime fitness and because many individuals attained large size but did not flower, I also analyzed "biomass," the mean dry weight of both above- and below-ground parts attained by each genotype in each environment. Any individuals that died before the experiment was terminated were represented with a dry weight of zero. The validity of this measure as a predictor of lifetime fitness depends on the assumption that future survival and fecundity will be positively correlated with current biomass. In addition to its value as a predictor of fitness, "biomass" provides a measure of each individual's propensity to spread vegetatively.

The traditional method of assessing environmental sensitivity is a technique known as "joint regression analysis" (Yates and

Cochran, 1938; Finlay and Wilkinson, 1963). The technique uses the mean performance of all genotypes in each environment as an estimate of that environment's "favorableness" (its "environmental value"). The environmental sensitivity of each genotype is represented as the regression of its performance on the environmental values (Falconer, 1981 p. 123). A genotype with average sensitivity will have a regression coefficient of 1, by definition. A regression coefficient significantly greater than 1 indicates a greater-than-average sensitivity to the environment (i.e., a genotype that performs unusually well in a "favorable" environment but does relatively poorly in less favorable ones). A value less than 1 indicates a lower-than-average environmental sensitivity, i.e., a genotype whose performance depends very little on the favorableness of the environment (as perceived by most other genotypes). This analysis has been widely used, especially by agronomists (Eberhart and Russell, 1966; Perkins and Jinks, 1968*a*, 1968*b*; Breese, 1969; Freeman and Dowker, 1973; Zuberi and Gale, 1976; see also Garbutt and Zangerl [1983]). Most recently, it has been used to compare the phenotypic plasticity of genotypes of *Agropyron repens* in populations of different ages (Taylor and Aarssen, 1988). However, significance testing rests on more than the usual assumptions of analysis of variance (Freeman, 1973), and the method has been criticized on statistical grounds (Freeman and Perkins, 1971; Freeman, 1973; Hill, 1975; Westcott, 1986). I have used this technique in conjunction with other methods of examining the data that are simpler and less assumption-bound.

The joint regression analysis proceeded as follows. The performance of each genotype in each environment was calculated. For each environment, these means were averaged over all genotypes to produce the "environmental value." Because the numbers of sexual and apomictic genotypes were not equal, means for the two groups were calculated separately and then averaged together. These values provided a measure of the overall favorableness of each environment and became the "independent" variable in the regression analysis. (The three performance measures produced different

environmental rankings.) A regression of performance on these environmental values was performed for each genotype, and the slopes of sexuals and apomicts were compared. The hypothesis that apomicts are more likely than sexuals to have slopes less than 1 was tested by a Fisher's exact test. This analysis was repeated for each performance measure.

Another way to test the hypothesis that apomictic genotypes are less sensitive to variation in their environment is to look at each genotype's variation in performance across the six environments. Unlike joint regression analysis, this method accommodates even those genotypes that respond idiosyncratically to the different environments, i.e., those that display a curvilinear rather than a linear response in the joint regression analysis or display no patterned response at all. In addition, this measure of stability is independent of the responses of the other genotypes.

To avoid confusing high sensitivity with high average performance, the measure of variation used must be independent of the sample mean. For flowering and biomass, there was a significantly positive correlation between a genotype's overall mean performance and the variance in its performance across environments (for flowering in sexual genotypes, $r = 0.818$, $N = 6$, $P < 0.05$; for flowering in apomictic genotypes, $r = 0.868$, $N = 14$, $P < 0.01$; for biomass, in sexual genotypes, $r = 0.819$, $N = 11$, $P < 0.01$; for biomass in apomictic genotypes, $r = 0.868$, $N = 14$, $P < 0.01$). Therefore, for these performance measures, I have used instead each genotype's coefficient of variation. This statistic was not correlated with mean performance (for flowering in sexual genotypes, $r = -0.625$, $N = 5$, $P > 0.05$; for flowering in apomictic genotypes, $r = -0.437$, $N = 14$, $P > 0.05$; for biomass in sexual genotypes, $r = -0.544$, $N = 11$, $P > 0.05$; for biomass in apomictic genotypes, $r = 0.128$, $N = 14$, $P > 0.05$). The lower the coefficient, the more "stable" was a genotype's response.

For the third measure of performance, survival, both variance and coefficients of variation were significantly negatively correlated with means; there was no transformation that produced a measure of varia-

tion that was independent of the mean. Therefore, I measured sensitivity by calculating each genotype's geometric mean survival over the six environments. The hypothesis that an apomictic genotype has lower environmental sensitivity than a sexual genotype predicts that it will be less likely to go extinct when faced with an unusually severe season. If one assumes that the six environments I have used represent a temporal series of six seasons and that performance in a particular environment is independent of a genotype's past history, then one predicts that apomictic genotypes are less likely to have a geometric mean fitness of zero in the experiment I have conducted.

Therefore, for each of the three measures, I calculated (for each genotype separately) mean performance in each of the six environments and the overall mean of these six means. For flowering and biomass, I present the coefficient of variation of these six means; for survival, I calculated the geometric mean of these six means. The test of significance used for means and CV's was a one-tailed Mann-Whitney *U* test comparing each measure's values for the sexual genotypes with those for the apomictic genotypes; the test of significance for geometric means was Fisher's exact test.

RESULTS

Joint Regression Analysis

Results of the joint regression analysis for survival are plotted in Figure 1. Note that the slopes for sexuals are steeper and that their y-intercepts are smaller than those of the apomicts. That is, the apomicts perceive any particular environment, especially those with lower environmental values, as more favorable than do the sexuals. There is a significant association of breeding system with slope, with apomictic genotypes much more likely than sexuals (71% vs. 18%) to have slopes less than 1, i.e., to have lower-than-average environmental sensitivity (Fisher's exact test, $P = 0.015$).

In the analysis for flowering (mean number of flower heads produced by survivors in each environment), I deleted the six sexual genotypes that completely failed to flower, since their "stability" is an artifact of this failure. Of the remaining genotypes, 43%

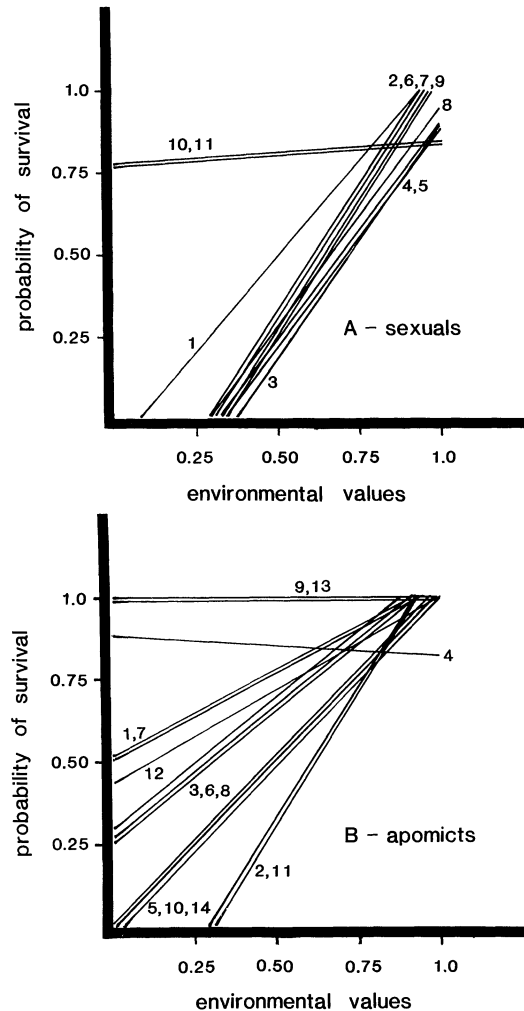


FIG. 1. Slopes of each genotype's regression of survival on the environmental value. An environment's "value" is calculated as the mean survival of all genotypes in that environment. The steeper the slope, the greater is a genotype's relative sensitivity to its environment. A) Slopes for the 11 sexual genotypes; B) slopes for the 14 apomictic genotypes.

of the apomicts and 80% of the sexuals had slopes less than 1; this difference is not significant (Fisher's exact test, $P = 0.303$).

The Fisher's exact test for biomass revealed no differences in slope between the two groups ($P = 0.689$): 50% of the apomictic genotypes and 64% of the sexual genotypes had slopes less than 1. Thus, while these results are inconclusive for two of the performance measures, the results for survival support the hypothesis that apomictic genotypes are less sensitive than are sexual

TABLE 1. A) Survival of each genotype in each of the six growth-chamber environments and arithmetic and geometric mean survival over all environments (see text). Numbers in parentheses are the numbers of replicates from which the overall means were calculated. At the bottom of each column is the mean of each parameter over all genotypes for each breeding system. Column headings refer to the different combinations of moisture and temperature as follows: C = cold, M = medium, H = hot, W = wet, D = dry. An "M" in the body of the table indicates that no replicate was present. B) Results of statistical tests (see text), comparing each column's values for apomicts (A) with those for sexuals (S), and environmental values for each environment.

A.		Environment						\bar{x} (N)	Geometric mean
Genotype	CD	CW	MD	MW	HD	HW			
Sexual:									
1	1.0	1.0	1.0	1.0	0.25	1.0	0.88 (24)	0.79	
2	0.67	1.0	1.0	1.0	0	1.0	0.78 (18)	0.00	
3	0.33	0.67	0.67	1.0	0	1.0	0.61 (18)	0.00	
4	1.0	1.0	0.5	1.0	0	0.5	0.67 (12)	0.00	
5	M	1.0	1.0	1.0	0	0	0.60 (6)	0.00	
6	1.0	1.0	1.0	1.0	0	1.0	0.83 (24)	0.00	
7	1.0	1.0	1.0	1.0	0	1.0	0.83 (6)	0.00	
8	1.0	1.0	0.5	1.0	0	0.75	0.71 (24)	0.00	
9	M	1.0	1.0	1.0	0	M	0.75 (4)	0.00	
10	0	1.0	1.0	1.0	1.0	1.0	0.83 (6)	0.00	
11	0	1.0	1.0	1.0	1.0	1.0	0.83 (6)	0.00	
Mean:	0.67	0.97	0.88	1.0	0.20	0.83	0.76	0.07	
Apomictic:									
1	1.0	1.0	1.0	1.0	0.67	1.0	0.95 (18)	0.93	
2	1.0	1.0	1.0	1.0	0	1.0	0.83 (12)	0.00	
3	1.0	1.0	1.0	1.0	0.5	1.0	0.92 (12)	0.89	
4	0.5	1.0	0.5	1.0	1.0	1.0	0.83 (12)	0.79	
5	1.0	1.0	0.89	1.0	0.33	1.0	0.87 (54)	0.82	
6	1.0	1.0	0.75	1.0	0.5	1.0	0.88 (24)	0.85	
7	1.0	1.0	1.0	1.0	0.67	1.0	0.95 (17)	0.93	
8	1.0	1.0	1.0	1.0	0.5	1.0	0.92 (12)	0.89	
9	1.0	1.0	1.0	1.0	1.0	1.0	1.00 (18)	1.00	
10	1.0	1.0	0.67	1.0	0.33	1.0	0.83 (18)	0.78	
11	1.0	1.0	0.5	1.0	0	1.0	0.75 (12)	0.00	
12	0.67	1.0	1.0	1.0	0.67	1.0	0.89 (17)	0.88	
13	0.9	1.0	1.0	1.0	0.1	1.0	0.83 (60)	0.67	
14	1.0	1.0	1.0	1.0	0.33	1.0	0.89 (18)	0.83	
Mean:	0.93	1.0	0.88	1.0	0.47	1.0	0.88	0.73	
B.		Environment						\bar{x}	Geometric mean
Results	CD	CW	MD	MW	HD	HW			
Means	A > S	A > S	A = S	A = S	A > S	A > S	A > S	A > S	
P	ns	ns	ns	ns	0.03	ns	0.002	0.0002	
Environmental value	0.80	0.99	0.88	1.0	0.34	0.92			

genotypes to the characteristics of their environment.

Variation in Performance Across Environments

The percentage of apomictic genotypes with nonzero values for geometric mean survival significantly exceeded that of sexuals (86% vs. 9%; Table 1; Fisher's exact test, $P = 0.0002$). For nearly all of the sexual genotypes, at least one of the environments

was completely unsuitable, typically the "hot-dry" environment. This is the one environment in which the mean survival of apomicts significantly exceeded that of sexuals (although all the environments mirrored this trend; see Table 1). The failure of many of the sexuals to survive the hot-dry environment contributes to the fact that the mean survival of the apomicts over all environments exceeded that of the sexual genotypes (Mann-Whitney U test, $U = 134$, $N_1 = 14$, $N_2 = 11$, $P = 0.003$). The envi-

TABLE 2. A) Mean number of flower heads produced per individual by survivors of each genotype in each of the six growth-chamber environments (abbreviations as in Table 1) and mean and coefficient of variation (CV) in flowering over all environments. A dash indicates that no individuals of that genotype survived to flower in that environment; an "M" indicates that no replicate of a particular genotype was present. B) Results of statistical tests comparing each column's values for apomicts (A) with those for sexuals (S) and environmental values for each environment.

A.		Environment						\bar{x} (N)	CV
Genotype	CD	CW	MD	MW	HD	HW			
Sexual:									
1	0.0	0.0	0.0	0.0	0.0	0.0	0.00 (21)	—	
2	0.0	0.0	0.0	0.3	—	0.0	0.07 (14)	1.89	
3	0.0	3.0	0.0	0.0	—	0.0	0.60 (11)	2.00	
4	0.0	0.0	0.0	0.0	—	0.0	0.00 (8)	—	
5	M	0.0	0.0	0.0	—	—	0.00 (4)	—	
6	0.0	2.0	0.0	0.0	—	0.0	0.40 (20)	2.00	
7	0.0	0.0	0.0	0.0	—	0.0	0.00 (5)	—	
8	0.0	1.0	0.0	0.0	—	0.0	0.20 (17)	2.00	
9	M	0.0	0.0	0.0	—	M	0.00 (3)	—	
10	—	0.0	1.0	0.0	0.0	0.0	0.75 (5)	1.11	
11	—	0.0	0.0	0.0	0.0	0.0	0.00 (5)	—	
Mean:	0	0.55	0.09	0.03	0	0	0.18	1.80	
Apomictic:									
1	2.3	4.0	0.0	3.7	0.0	2.0	2.0 (17)	0.79	
2	0.0	2.0	0.0	0.0	—	0.0	0.40 (10)	2.00	
3	0.0	1.0	0.0	0.0	0.0	0.0	0.17 (11)	2.19	
4	0.0	8.0	0.0	0.0	0.0	0.0	1.33 (9)	2.24	
5	0.0	0.4	0.0	0.3	0.0	0.0	0.13 (47)	1.42	
6	0.0	0.8	0.0	0.8	0.0	0.0	0.25 (21)	1.41	
7	0.0	2.0	0.3	11.0	0.0	0.0	2.22 (16)	1.80	
8	0.0	0.0	0.0	0.0	0.0	0.5	0.08 (11)	2.33	
9	0.0	0.0	0.0	3.7	0.0	0.0	0.61 (18)	2.24	
10	0.0	4.3	2.0	4.0	0.0	0.0	1.72 (15)	1.09	
11	0.0	0.0	0.0	9.0	—	0.0	1.80 (10)	2.00	
12	0.0	12.0	0.0	4.3	0.0	1.7	3.0 (15)	1.44	
13	0.0	1.4	0.0	0.3	0.0	0.0	0.28 (50)	1.83	
14	0.0	3.3	0.0	0.0	0.0	0.0	0.56 (16)	2.22	
Mean:	0.17	2.80	0.17	2.65	0	0.30	1.04	1.79	
B.		Environment						\bar{x}	CV
Results	CD	CW	MD	MW	HD	HW			
Means	A > S	A > S	A > S	A > S	A = S	A > S	A > S	A < S	
P	NS	0.020	NS	0.010	NS	NS	0.004	NS	
Environmental value	0.09	1.68	0.13	1.34	0	0.15			

ronmental values indicate that all of the environments except hot-dry were approximately equally favorable; survival in the hot-dry environment was depressed for both sexuals and apomicts, but more so for sexuals.

These differences in survival and in its geometric mean are not simply a result of the difference in sample size between sexual and apomictic genotypes (each sexual genotype was represented by an average of 2.3

replicates in each environment, while apomictic genotypes were replicated, on average, 3.4 times). To determine this, I created three separate random samples from the population of apomictic replicates by randomly drawing a single replicate from the available replicates for each genotype in each environment and recalculating arithmetic and geometric means for each sample. This is an extremely conservative test, since it allows each apomictic genotype's perfor-

TABLE 3. A) Mean biomass (g) of each genotype in each of the six growth-chamber environments (abbreviations as in Table 1) and mean and coefficient of variation in biomass over all environments. An "M" in the body of the table indicates that no replicate was present. B) Results of Mann-Whitney U tests comparing each parameter's values for apomicts (A) with those for sexuals (S) and environmental values for each environment.

A.	Genotype	Environment					\bar{x} (N)	CV	
		CD	CW	MD	MW	HD			HW
Sexual:									
	1	1.71	5.17	2.10	5.40	0.33	3.40	3.02 (24)	0.61
	2	1.11	4.13	2.42	5.12	0.00	5.36	3.02 (18)	0.66
	3	0.45	1.01	0.47	3.26	0.00	3.34	1.42 (18)	0.96
	4	1.02	2.68	0.54	2.69	0.00	0.69	1.27 (12)	0.82
	5	M	0.85	0.34	1.46	0.00	0.00	0.53 (6)	1.06
	6	0.98	1.80	1.54	4.12	0.00	3.60	2.01 (24)	0.71
	7	0.60	1.59	0.78	1.72	0.00	2.21	1.15 (6)	0.65
	8	1.36	2.12	0.67	3.29	0.00	1.88	1.55 (24)	0.68
	9	M	0.91	3.42	2.55	0.00	M	1.72 (4)	0.78
	10	0.00	1.02	0.21	0.83	0.40	2.95	0.90 (6)	1.09
	11	0.00	1.81	0.65	5.84	0.65	6.16	2.52 (6)	1.00
	Mean:	0.80	2.10	1.20	3.30	0.13	2.96	1.74	0.82
Apomictic:									
	1	2.41	2.17	1.36	4.75	0.71	4.72	2.69 (18)	0.58
	2	1.82	4.03	1.13	3.38	0.00	4.04	2.40 (12)	0.64
	3	1.63	1.51	1.17	4.67	0.58	1.59	1.86 (12)	0.70
	4	1.21	4.46	0.57	4.51	0.51	3.50	2.46 (12)	0.71
	5	2.01	4.63	1.73	5.99	0.44	4.25	3.18 (54)	0.60
	6	2.04	3.79	1.40	3.41	0.61	3.05	2.38 (24)	0.48
	7	1.27	2.51	1.93	3.58	0.93	3.28	2.25 (17)	0.43
	8	2.08	3.49	2.01	3.92	0.54	3.49	2.59 (12)	0.45
	9	1.19	2.33	1.45	3.10	0.95	4.02	2.17 (18)	0.51
	10	2.37	3.83	1.17	4.94	0.49	3.54	2.82 (18)	0.52
	11	1.70	4.48	0.59	5.87	0.00	5.21	2.98 (12)	0.77
	12	0.70	2.79	1.07	3.67	0.85	3.34	2.07 (17)	0.59
	13	1.35	1.65	1.41	2.87	0.05	2.11	1.57 (60)	0.54
	14	2.70	7.10	2.68	7.07	0.36	5.78	4.28 (18)	0.59
	Mean:	1.75	3.48	1.45	4.41	0.50	3.71	2.55	0.58
B.									
	Results	Environment					\bar{x}	CV	
		CD	CW	MD	MW	HD			HW
	Means	A > S	A > S	A > S	A > S	A > S	A > S	A > S	A < S
	P	0.001	0.011	NS	0.038	0.002	NS	0.001	0.0003
	Environmental value	1.28	2.79	1.33	3.86	0.32	3.34		

mance in each environment to be represented by only one replicate. All trends remained the same: in all three random samples, arithmetic and geometric mean apomictic survival exceeded that of sexuals (significantly so in two of the three samples). For arithmetic means, $U = 130$ ($P = 0.002$), $U = 119$ ($P = 0.018$), $U = 104.5$ ($P = 0.116$); for geometric means, $U = 106$ ($P = 0.046$), $U = 106$ ($P = 0.046$), $U = 88$ ($P = 0.367$).

There was no difference between the two groups in their mean coefficients of variation for flowering. However, mean flower-

head production by apomicts in each environment always equalled or exceeded that of sexuals in that environment (Table 2); this difference was statistically significant in two of six environments. Overall mean flower-head production by apomictic genotypes exceeded that of sexuals (Mann-Whitney U test, $U = 130.5$, $N_1 = 14$, $N_2 = 11$, $P = 0.004$). The fact that six of the 11 sexual genotypes failed to flower contributes substantially to this difference; however, even those sexual genotypes that flowered never achieved the rates of flower-head pro-

duction achieved by some of the apomicts. Environmental values indicate that wet environments promoted flower production more than dry ones.

Finally, apomicts had a significantly lower average coefficient of variation (CV) for biomass (0.58 vs. 0.82; Mann-Whitney U test, $U = 139.5$, $N_1 = 14$, $N_2 = 11$, $P = 0.0007$). Not only were they less variable, but they also, on average, attained larger masses than did sexual genotypes (Table 3). In each of the individual environments, mean biomass for apomictic genotypes exceeded that for sexual genotypes (four of six differences were statistically significant). Mean overall biomass for apomicts also exceeded that for sexuals (Mann-Whitney U test, $N_1 = 14$, $N_2 = 11$, $P = 0.023$).

Once again, these differences cannot be attributed simply to differences in sample size. The three randomly drawn apomictic samples showed the same trends seen in the entire data set, with apomictic mean biomass significantly exceeding sexual biomass in all three draws ($U = 126$, 119.5, 122; all $P \leq 0.021$) and with apomictic CV's always lower than sexual CV's, (significantly so in two of the three samples; Mann-Whitney U tests; $U = 120.5$, 131.5, 99.5; $P = 0.019$, 0.003, and 0.228, respectively).

DISCUSSION

These results support the hypotheses that the performance of apomictic genotypes is typically less sensitive to variation in the environment than is the performance of sexual genotypes and that apomicts are less likely to go extinct when faced with environmental extremes. The two methods of analysis produced consistent results. Though the joint regression analysis failed to find any differences between the two groups of genotypes with regard to flowering or biomass, it did demonstrate that the survival of apomictic genotypes is less likely to be adversely affected by their environment than is the survival of sexuals. The comparison of geometric mean survival for the two groups produced the same result, implying that apomictic genotypes are less likely to go extinct during a particularly extreme season. Curiously, the environment in which sexuals were most disadvantaged relative to

apomicts was the hot-dry environment, the one most like those at lower elevations and lower latitudes, where sexuals are most common.

Apomicts displayed lower coefficients of variation across environments for biomass, which further supports the notion that they are relatively insensitive to their environment. But in addition to their lower sensitivity, they also have a higher overall mean biomass. In nearly every environment, apomicts grew larger than sexuals—in the favorable wet and warm environments, as well as in the less favorable dry and cool ones. They also displayed a nearly ten-fold higher mean rate of flower production. Under these circumstances, it is hardly even necessary that they be less sensitive in order to be regarded as “general-purpose genotypes.”

While these results show apomicts to be clearly more “tolerant” of environmental variability than sexual genotypes, the mechanisms conferring this tolerance remain obscure. *Antennaria*'s intractability to electrophoretic analysis (Bierzychudek, unpubl.) has prevented any estimate of the degree of relatedness between mates and has foiled any test of the hypothesis that apomictic genotypes are more highly heterozygous. However, even if higher levels of heterozygosity were to be found in apomicts, it would be impossible to prove that such heterozygosity is in fact responsible for conferring their broad tolerance. Further work is necessary to discover the generality of this finding and the mechanisms responsible for it.

Theory that attempts to explain the widespread occurrence of sexual reproduction is typically predicated on the assumption that asexual and sexual genotypes are fundamentally similar except for the sexual genotypes' ability to produce genetically diverse progeny. This study suggests that there may be other ecological differences between sexuals and asexuals that need to be considered in such theory. In the present instance, these differences provide an explanation for the phenomenon of geographic parthenogenesis; they indicate that apomictic genotypes can tolerate a wider range of environments with less depression of their performance than can sexual genotypes.

However, these results do not correspond particularly well with the patterns of geographic distribution exhibited by sexuals and apomicts. Because sexuals are excluded from high elevations and high latitudes, we might expect that the apomicts would outperform sexuals only in the cooler environments. But in fact, apomicts do better than sexuals in all of the environments, even under the warmest, driest conditions. If apomicts are so clearly superior to sexual genotypes and so little prone to extinction, how is it that mixed populations of sexuals and apomicts manage to persist? To answer this question, experiments exploring the existence of other differences between sexual and apomictic *Antennaria* are currently underway.

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