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Differentiation in reproductive strategy between sexual and asexual populations of *Antennaria parlinii* (Asteraceae)

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ABSTRACT

Plants exhibit wide variation in reproductive traits, and these traits often covary to form distinct strategies. Uniparental reproduction via self-fertilization is often associated with high reproductive effort and enhanced seed dispersal, the combination of which is viewed as an adaptive strategy in ephemeral or disturbed habitats. We investigated the hypothesis that uniparental reproduction via asexual apomixis is associated with a similar suite of traits and more frequent occurrence in disturbed habitats among populations of *Antennaria parlinii*, a dioecious species that exhibits wide variation in sexuality at the population level. By comparing 18 sexual and 21 asexual populations in Ohio, USA, we found that, as predicted, sexual populations were more likely to occur in wooded habitats than asexual populations, which were found more frequently in disturbed roadside ditches and fallow fields. As expected, plants in asexual populations produced, on average, twice as many seeds per inflorescence as plants in sexual populations. Asexual plants also exhibited much higher reproductive effort than sexual plants when compared in a common greenhouse environment, indicating a genetic basis for the difference in reproductive output observed in natural populations. Seeds of *A. parlinii* are equipped with plume-like pappus that enhances wind dispersal. Settling velocity in still air was lowest for diaspores with long, highly barbed pappus bristles and small seeds. Compared to sexual populations, asexual populations produced diapsores with longer, more highly barbed pappus and smaller seeds. Taken together, our results suggest that divergent selective pressures in different habitats have produced two distinct reproductive strategies in *A. parlinii*.

Keywords: anemochory, apomixis, asexuality, habitat disturbance, plant reproduction, pussytoes, reproductive effort, seed dispersal, sex.

INTRODUCTION

As a group, flowering plants exhibit wide variation in traits related to major components of reproduction, such as pollination, seed production and seed dispersal. These reproductive traits often exhibit non-random patterns of covariation. Individual traits (or 'tactics')

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co-occur in distinct reproductive syndromes (or 'strategies') that recur among species (Grime, 1977; Southwood, 1988). The component tactics of a reproductive strategy presumably function in an integrated way to maximize fitness under certain ecological conditions.

Despite the developmental and functional linkages among reproductive characters, reproductive variation is often studied on a trait by trait basis (Primack, 1987; Barrett *et al*., 1997). However, the fitness consequences of a particular trait may depend on the traits that it is associated with (e.g. Morgan *et al*., 1997). As a result, micro-evolutionary analysis is best performed by viewing individual traits in the broader context of the reproductive strategy, life history and ecology.

The most fundamental axis of reproductive variation in plants involves the contrast between biparental reproduction via sex and outcrossing versus uniparental reproduction via self-fertilization or apomixis (asexuality; Fryxell, 1957). Associations between selfing and other reproductive and life-history traits have been widely studied; however, we have very little information on the reproductive strategies of apomicts. Moreover, it is not clear how much selection can modify reproductive traits once apomixis has evolved, given that asexuality does not produce recombinational variation upon which selection may act. Given that apomixis and selfing are both modes of uniparental reproduction, we might expect apomixis to be associated with the syndrome of traits that generally characterize selfing taxa. The aim of this study is to test this hypothesis.

Comparisons between closely related selfers and outcrossers reveal changes in many reproductive and life-history characters that appear to accompany the evolution of selfing (Ornduff, 1969). Selfers tend to be annuals more often than outcrossers (Grant and Grant, 1965; Lloyd, 1980; Barrett and Eckert, 1990; Barrett *et al*., 1997). Annuals, in turn, usually exhibit a greater per-season reproductive effort than perennials (Silvertown and Dodd, 1997). There may also be an association between the selfing strategy and habitat. Selfers are often disproportionately common in unsaturated or disturbed habitats (reviewed in Lloyd, 1980; but see Jain, 1976). Species occurring in disturbed habitats often produce seeds with greater dispersal potential than species in stable habitats (e.g. Werner and Platt, 1976; Platt and Weiss, 1977; Schulz *et al*., 1991; Andersen, 1992). Selfing, high fecundity and enhanced seed dispersal are viewed as major components of a 'ruderal' strategy (Grime *et al*., 1988). Stronger evidence for the functional significance of trait–trait and trait–habitat associations revealed by interspecific comparisons can be obtained by examining patterns of covariation among populations within species (e.g. Morishima and Barbier, 1990; Morishima *et al*., 1992).

The trait associations that typify a ruderal strategy are also predicted by life-history and metapopulation theory. Frequent extinction and recolonization in a metapopulation should select for increased seed dispersal ability (reviewed in Olivieri and Gouyon, 1997). This prediction has rarely been tested (Olivieri *et al*., 1983; Peroni, 1994). Life-history theory predicts that increased fecundity is selected at the expense of adult survival in early successional habitats where seedling recruitment is frequent relative to late successional habitats (Young, 1990). Metapopulation models make a similar prediction; however, the situation becomes more complex when dispersal is also allowed to evolve (Olivieri and Gouyon, 1997). To date, no-one has jointly examined differences in reproductive mode, fecundity and seed dispersal ability between conspecific populations in different habitats.

One of the main hurdles in evaluating trait–trait and trait–habitat associations in apomictic plants is that apomixis is often associated with polyploidy. Apomictic taxa

usually have larger geographical ranges and occur at higher altitudes and latitudes, and in more disturbed habitats, than closely related sexual taxa (Bierzychudek, 1987a; Asker and Jerling, 1992; see also Glesener and Tilman, 1978; Bell, 1982; Lynch, 1984). This may be due to the reproductive assurance afforded by uniparental reproduction (Stebbins, 1950; Bierzychudek, 1990), but it may also be a direct consequence of polyploidy, because increased ploidy may enhance ecological amplitude through slower development, delayed reproduction, longer life span, larger seeds and greater chemical defence against pests and pathogens (Levin, 1983; Bierzychudek, 1987a). Differences in ploidy may also underlie variation in other reproductive and life-history traits (Levin, 1983).

In this study, we avoid the confounding effects of variation in ploidy by investigating covariation between asexuality and other components of reproductive strategy among populations of *Antennaria parlinii* Fern, a species consisting of both sexual and asexual populations with the same ploidy level. It is distributed throughout the central and southern parts of eastern North America, and is near uniformly hexaploid ($2n = 6x = 86$; Bayer and Stebbins, 1981, 1987; Bayer, 1984). Sexual plants are dioecious, whereas asexual plants are female and produce seed through autonomous, mitotic diplosporous apomixis (Stebbins, 1932).

Based on the geographical distribution of males indicated by herbarium specimens, populations in the southern and western portions of the species' range are predominantly sexual, whereas populations in the eastern and northern parts of the range are predominantly asexual (Bayer, 1980; O'Connell, 1997). Populations between these two zones may vary widely in sexuality. For instance, Bayer and Stebbins (1983) found wide variation in sex ratio among populations in Ohio, USA, from populations consisting of females only to populations consisting of both males and females. We investigated these Ohio populations in more detail and found that sex ratio is a reliable indicator of sexuality. By combining population surveys of seed production with pollination experiments in both the field and greenhouse, we showed that females from populations containing both sexes were obligately sexual, whereas those from populations containing females only were obligately asexual (O'Connell and Eckert, 1999).

In this study, we test the hypothesis that sexual and asexual *A. parlinii* exhibit differences in reproductive strategy related to habitat. First, we test the hypothesis that asexual plants occur in habitats that are more frequently disturbed than those in which sexual plants are commonly found by determining the reproductive mode and habitat type for 39 populations of *A. parlinii* in Ohio. We then compare the reproductive output of nine sexual and 15 asexual populations in both natural populations and in a common greenhouse environment. Finally, we test the prediction that asexuality is associated with enhanced seed dispersal potential. The wind-dispersed seeds of *A. parlinii* are equipped with a plume-like pappus that keeps the seed aloft during dispersal. We determine which diaspore characteristics decrease seed settling velocity, and then compare these traits between nine sexual and 15 asexual populations.

METHODS AND MATERIALS

Study populations

We studied 39 populations in Ohio, USA (Fig. 1), two in Frontenac and Leeds and Grenville Counties, eastern Ontario, Canada (KL and QU), and another in Gatineau

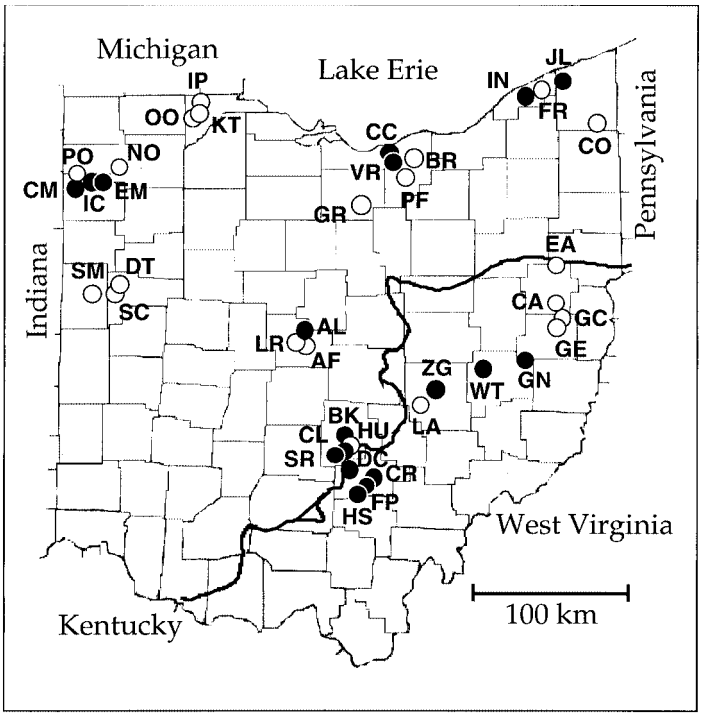


Fig. 1. Location of *Antennaria parlinii* populations in Ohio used in this study. ● = sexual populations ($n = 18$), ○ = asexual populations ($n = 21$). The dark line is the southern limit of the Wisconsin glaciation.

County, western Québec, Canada (FG). Most populations had distinct boundaries and were separated from nearby populations by at least 2 km. Previous field and greenhouse pollination experiments involving 24 of these populations demonstrated that sex ratio is a reliable indicator of reproductive mode. Plants from populations including both males and females are obligately sexual, whereas those from populations consisting of females only are obligately asexual (O'Connell and Eckert, 1999). In Ohio, 18 populations contained both males and females and were, therefore, considered sexual; 21 included females only and were considered asexual. The three Canadian populations contained females only and were considered asexual. All plants were identified as *A. parlinii* following Bayer and Stebbins (1993). The locations of all populations are in O'Connell (1997), and voucher specimens are in the Fowler Herbarium (QK) at Queen's University.

Habitat

We quantified differences in habitat between 18 sexual and 21 asexual populations of *A. parlinii* in Ohio (Fig. 1) by recording, for each population, the presence or absence of a tree canopy as an index of habitat successional stage and noting the general habitat type (roadside, riverside, lakeside, field or cemetery). Thirty of the 39 populations occurred close to roads, and for these we noted the steepness of the slope on which they occurred (flat, gently sloped or steep), because flat or gently sloped roadsides were more likely

to be mowed or otherwise disturbed than steeply sloped roadsides. We assessed associations between reproductive mode (sexual *vs* asexual) and habitat characteristics using chi-squared tests.

Reproductive output

We compared reproductive output between nine of the sexual populations from Ohio (AL, CC, CM, CR, GN, HS, IN, JL and SR; Fig. 1) and 15 asexual populations, including 12 from Ohio (AF, BR, FR, GC, GR, HU, IP, KT, OO, PF, SM and SC) plus three from Canada (FG, KL and QU). This is the same set of populations we previously studied to investigate differentiation for sexuality (O'Connell and Eckert, 1999). Although the Canadian populations are geographically separated from the asexual populations in Ohio, they were not distinct from the Ohio populations for any of the traits examined (analysis not shown). To investigate whether sexual and asexual populations differed in reproductive output, we sampled approximately 20 inflorescences just before seed dispersal from each of the nine sexual populations ($n = 199$ inflorescences in total) and 15 asexual populations ($n = 292$). In some populations, individual plants were difficult to distinguish because of stoloniferous growth. Accordingly, we collected inflorescences at 2-m intervals to minimize sampling from the same individual more than once (following Bayer, 1980).

For each inflorescence, we counted the number of capitula, plus the seeds and florets in the central capitulum, and calculated capitula per inflorescence, florets per capitula, seeds per floret, seeds per capitulum and seeds per inflorescence. We then used nested analysis of variance (ANOVA) to assess differences in reproductive output between sexual and asexual populations. Population reproductive type (sexual *vs* asexual) was a fixed effect and population (nested within reproductive type) was a random effect. Because we sampled an unequal number of sexual and asexual populations, and an unequal number of inflorescences from each population, the denominator mean squares and degrees of freedom for the various *F*-tests were adjusted using the Satterthwaite method (Sokal and Rohlf, 1995, pp. 292–300). Residual analysis indicated departures from assumptions of ANOVA for all variables. Accordingly, the data were transformed to meet assumptions. Seeds per floret was arcsine-transformed ($Y' = 2\arcsin\sqrt{Y}$). The other four variables were transformed ($Y' = Y^{\lambda}$) using the Box-Cox method (Sokal and Rohlf, 1995, pp. 417–419). The appropriate value of λ was 0.2 for capitula per inflorescence, 0.6 for florets per capitulum, 0.8 for seeds per capitulum and 0.4 for seeds per inflorescence. These and other analyses reported below were performed using JMP (Version 3.2.1, SAS Institute, 1997).

To determine whether seeds from sexual and asexual populations differ in viability, we compared their germination in a common growth chamber environment. We randomly sampled 20 seeds per inflorescence from each of approximately 19 inflorescences from each of the nine sexual populations ($n = 177$ inflorescences in total) and 15 asexual populations ($n = 239$). Seeds ($n = 8337$ in total) were placed in sterile petri dishes on filter paper moistened with deionized water and stored for 4 weeks at 4°C, after which they were germinated in growth chambers at 22°C during 14 h light and at 16°C during 10 h dark. Germination was scored daily until few new seedlings (< 0.5%) were observed (10 days). We assessed the difference in total germination between sexual and asexual populations using nested ANOVA (as above). The proportion of seeds germinated was arcsine-transformed to meet assumptions of ANOVA.

Reproductive output in a common greenhouse environment

We compared the reproductive behaviour of sexual and asexual plants in a common greenhouse environment to determine the extent to which differences in reproductive output between sexual and asexual populations observed in the field had a genetic basis. In August 1996, plants from the populations previously sampled for measures of reproductive output and seed dispersal potential (see above) were collected, transplanted into sterile potting medium and randomly arranged in an outdoor garden in Kingston, Ontario, Canada. We sampled 20 plants from each asexual population and 30 from each sexual population. By autumn, the plants were dormant and overwintered in a dark coldroom (5°C). The following March, we randomly arranged the plants on a single greenhouse bench under ambient light and temperatures of 15–30°C.

Ninety-one females from 13 asexual populations and 33 females (plus 29 males) from nine sexual populations flowered. Some populations were represented by only one or two flowering individuals, so we could assess general differences among sexual and asexual plants but not variation among populations within population reproductive types. For each plant, one inflorescence was left unpollinated. On plants that produced at least two inflorescences, another was hand-pollinated using pollen provided by a male from a different population. Inflorescences were collected just before seed dispersal. For each flowering plant, we counted the number of capitula produced by each inflorescence. For each inflorescence that set at least one seed, we counted the total number of florets produced by the whole inflorescence and divided that by the number of capitula to yield the average number of florets per capitulum for that inflorescence. For plants that produced two inflorescences, the two values for each variable (capitula per inflorescence, florets per capitulum and florets per inflorescence) were averaged. Because the data departed significantly from a normal distribution and sample sizes were highly unbalanced, we compared these measures of reproductive effort between sexual and asexual plants using the non-parametric Wilcoxon two-sample test (Sokal and Rohlf, 1995, pp. 427–431) with a one-tailed test of significance (H_A: asexual > sexual).

Seed dispersal

The pappus on an *A. parlinii* seed acts as a parachute to slow the seed down as it falls, presumably enhancing the potential for dispersal. The settling velocity of a diaspore is expected to correlate negatively with pappus characteristics that increase the size or effectiveness of the parachute, and positively with seed size. To test if seeds from sexual and asexual populations differ in dispersal potential, we measured four traits on a sample of four diaspores (Fig. 2) from approximately 19 inflorescences for each of the nine sexual populations ($n = 193$ inflorescences in total) and 15 asexual populations ($n = 255$) in which we quantified reproductive output (see above). For each diaspore, we counted the number of pappus bristles and scored the extent to which bristles were barbed (a combination of number and size of barbs) on a subjective scale of 1 to 5. We also measured the length of three pappus bristles per diaspore, the length of each seed twice, and the width of each seed at four different locations along its length. All measurements were made using a Leica M3Z™ stereo dissecting microscope with a drawing tube mounted over a CalComp DrawingBoard II™ digitizing tablet. Tracings were measured using the public domain software NIH Image (Version 1.59; Rasband, 1993) with a calibration of 39.55 pixels per

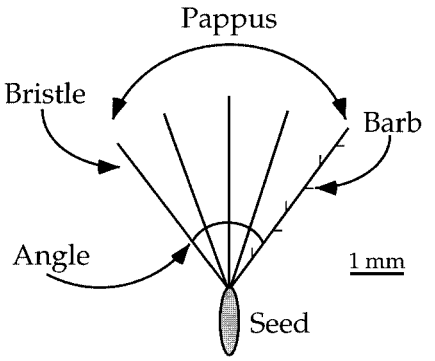


Fig. 2. Traits potentially contributing to the dispersal ability of an *Antennaria parlinii* diaspore.

millimetre and a pixel aspect ratio of 1.19. For each diaspore, we calculated averages for pappus length, seed length and seed width, and then calculated seed size (width × length). We then averaged the values for the four diaspores per inflorescence to yield one value for each variable per inflorescence. All measurements were done blind to the identity of the plant and population that the diaspore came from. Not all measurements were made for each diaspore, so sample sizes differ among variables.

We used nested ANOVA (as above) to assess differences in the four diaspore traits between sexual and asexual populations. For analyses involving pappus length and seed size, residual analysis indicated small but significant departures from assumptions of ANOVA. No transformation of the data alleviated this problem. However, the differences between sexual and asexual populations were so large that the effect of population type remained highly significant even when the data were rank-transformed (Conover, 1980). Moreover, all significant contrasts between sexual and asexual populations remained highly significant when population means were compared using *t*-tests or non-parametric Wilcoxon tests. Thus, the results presented below are probably robust to violation of ANOVA assumptions.

Free-fall tests

We determined whether the diaspore characteristics measured above (number of pappus bristles, barb score, pappus length and seed size) correlated with diaspore settling velocity. Fifty-five diaspores with different combinations of the four traits were selected from among the inflorescences that provided the diaspores measured above. We dropped each diaspore six times in still air from a height of 80 cm inside a 35-cm diameter cardboard tube, recorded how long it took to reach the floor, and calculated average settling velocity from the six replicate trials. The angle the pappus was open (Fig. 2) was measured just before dropping each diaspore. The other four traits were measured as above for each diaspore after the free-fall test. Again measurements were made blind to which inflorescence or population the diaspore came from and its settling velocity.

We tested whether settling velocity was related to any of the five diaspore traits using Pearson correlations. We then used multiple regression to estimate the relative effect of each of the diaspore traits that correlated individually with settling velocity. There were no

significant correlations among these traits (mean absolute $r = 0.13$, range = –0.17 to +0.24, all $P > 0.07$), and variance inflation factors were all less than 1.2. Consequently, multiple collinearity was not a problem in interpreting the results of the multiple regression analysis.

The multiple regression equation was used to estimate settling velocity from diaspore characteristics for all the diaspores measured in the population survey described above. A pappus angle of 90° was used for all diaspores because it was the average angle in the free-fall test and pappus angle appeared to be a characteristic of how diaspores were stored rather than what population they came from. We used nested ANOVA (as above) to assess the difference in estimated settling velocity between sexual and asexual populations. Again, residual analysis indicated minor departures from assumptions of ANOVA. However, the effect of population reproductive type remained highly significant in all alternative analyses (see above), thus the results presented below are probably robust to violation of ANOVA assumptions.

RESULTS

Habitat

Sexual and asexual populations of *A. parlinii* tended to occur in different habitats in Ohio (Table 1). Populations in open habitats were significantly more likely to be asexual (71% of 21 populations) than populations in habitats with a tree canopy (33% of 18 populations; 2×2 contingency table $\chi^2 = 5.7$, d.f. = 1, $P = 0.017$). Among the 30 populations located along roadsides (including 16 open and 14 canopied populations), asexual populations were more frequent on flat (5 asexual populations *vs* 1 sexual population) or gently sloped roadsides (10 asexual populations *vs* 3 sexual populations), which were mowed or otherwise disturbed more regularly, than steeply sloped roadsides, which tended to be disturbed infrequently (3 asexual *vs* 8 sexual; 2×3 contingency table $\chi^2 = 8.0$, d.f. = 2, $P = 0.018$). This pattern was independent of the association between reproductive mode and tree canopy, as the incline of roadside populations was not related to whether they were under a canopy (2×3 contingency table $\chi^2 = 2.7$, d.f. = 2, $P = 0.26$). Of the nine populations that were not close to a road, asexual populations were more common in open, disturbed habitat such as lawns, cemeteries and fallow fields (3 asexual *vs* 2 sexual) than river valleys with tree cover (0 asexual *vs* 4 sexual).

Table 1. The occurrence of sexual and asexual populations of *Antennaria parlinii* in different habitats in Ohio[a]

Habitat type	Tree canopy	Open
Roadsides	8/6	4/12
River valley	4/0	0/0
Disturbed field	0/0	2/3

[a] The entry in each cell is the number of sexual populations/number of asexual populations found in that habitat category.

Reproductive output

Four of five measures of reproductive output were significantly higher in asexual than sexual populations (Fig. 3; Table 2). Compared to plants from sexual populations, plants from asexual populations had almost two more capitula per inflorescence (6.9 ± 0.33 *vs* 5.1 ± 0.30; mean ± standard error), 32% more florets per capitulum (162.9 ± 8.4 *vs* 123.7 ± 6.3), but about the same number of seeds per floret (0.73 ± 0.04 *vs* 0.69 ± 0.04). Overall, plants in asexual populations produced 30% more seeds per capitulum (120.2 ± 8.4 *vs* 83.5 ± 4.9) and twice as many seeds per inflorescence (876.3 ± 74.5 *vs* 439.9 ± 43.5).

The proportion of seeds germinating averaged 0.40 ± 0.04 for 15 asexual populations and 0.34 ± 0.06 for nine sexual populations (Fig. 4). Nested ANOVA detected a significant difference in germination among populations within reproductive types but not between reproductive types (Table 2). The rate of germination in both sexual and asexual populations was similar throughout the duration of the experiment (Fig. 4).

Differences in reproductive effort persisted when plants from sexual and asexual populations were grown and pollinated in a common greenhouse environment. Compared to plants from sexual populations, plants from asexual populations produced almost 1.5 more capitula per inflorescence (5.00 ± 0.20, $n = 91$ *vs* 3.68 ± 0.25, $n = 33$; one-tailed Wilcoxon test, $P = 0.0002$), 12% more florets per capitulum (103.7 ± 2.7, $n = 91$ *vs* 92.3 ± 6.3, $n = 17$; $P = 0.031$) and 38% more florets per inflorescence (517.7 ± 25.1, $n = 91$ *vs* 375.4 ± 58.9, $n = 17$; $P = 0.009$).

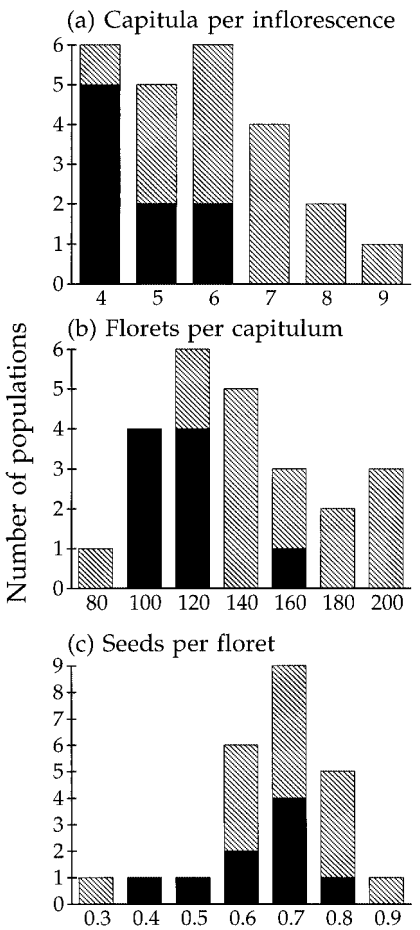
Relation between diaspore dispersal traits and settling velocity

The settling velocity of *A. parlinii* diaspores correlated negatively with three of four pappus traits (Fig. 5). Settling velocity decreased with angle of pappus opening ($r = -0.47$, $P = 0.0003$), barb score ($r = -0.40$, $P = 0.0027$) and pappus length ($r = -0.39$, $P = 0.0031$), increased with seed size ($r = +0.52$, $P = 0.0001$), but did not vary with pappus number ($r = +0.16$, $P = 0.23$).

A multiple regression including the joint effects of pappus angle, barb score, pappus length and seed size on diaspore settling velocity was highly significant (Table 3). Partial regression coefficients for pappus angle, barb score and pappus length were all significant and negative; the coefficient for seed size was significant and positive. The standardized effects of all variables on settling velocity were roughly equal.

Diaspore dispersal traits

Traits that reduced diaspore settling velocity were greater in asexual than sexual populations (Fig. 6; Table 4). Diaspores from asexual populations had a higher barb score than those from sexual populations (3.18 ± 0.14 *vs* 2.27 ± 0.11), and pappus bristles were 8% longer in asexual than sexual populations (7.06 ± 0.076 *vs* 6.52 ± 0.078 mm). Similarly, seed size, which correlated positively with settling velocity, was 11% smaller in asexual than sexual populations (0.418 ± 0.010 *vs* 0.463 ± 0.007 mm^2). The number of pappus bristles per seed, the single trait that did not influence seed settling velocity, did not differ between asexual and sexual populations (22.1 ± 0.4 *vs* 22.0 ± 0.5). Estimated settling velocity for diaspores from asexual populations was 12% lower than those from sexual populations (0.198 ± 0.0027 *vs* 0.225 ± 0.0033 $m \cdot s^{-1}$; Fig. 7).



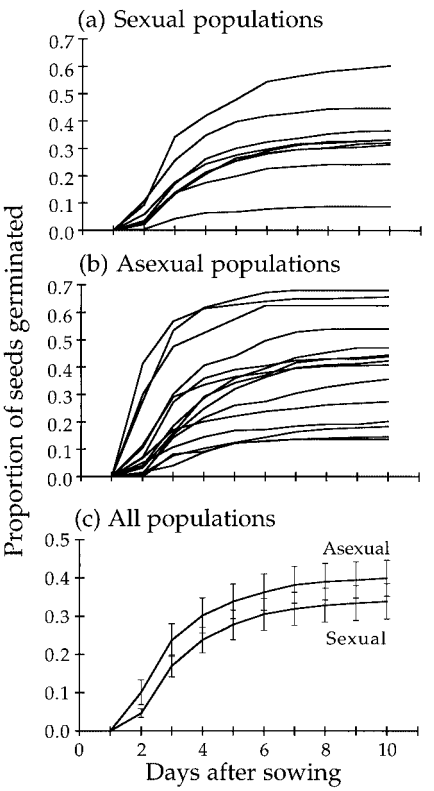


Fig. 3. (**Left**) Distribution of population means for three components of reproductive output for nine sexual (■) and 15 asexual (▨) populations of *Antennaria parlinii*. Summary statistics by population type are in the text. Analysis of these data is in Table 2.

Fig. 4. (**Right**) Germination of seeds from nine sexual and 15 asexual populations of *Antennaria parlinii* in a growth chamber. In (a) and (b), the lines are individual populations. In (c), the lines show the means of population means, and the error bars are ± 1 standard error. Analysis of these data is in Table 2.

DISCUSSION

Antennaria parlinii exhibits striking variation in reproductive mode. Some populations are obligately sexual, whereas others reproduce asexually via apomixis (Bayer and Stebbins, 1983; O'Connell and Eckert, 1999). The results of this study reveal strong covariation between reproductive mode (sexual *vs* asexual) and other major components of reproductive strategy in this species. Compared to sexual *A. parlinii*, asexual ramets produced twice as many seeds per inflorescence (Fig. 3); and the seeds produced by asexual ramets

Table 2. Analysis of variance of reproductive output between nine sexual and 15 asexual populations of *Antennaria parlinii* with reproductive type (sexual *vs* asexual) as a fixed effect and population (nested within reproductive type) as a random effect

Variable[a]	r^2	Effect (d.f.) Repro. type (1) $F(P)$	Pop'n (22) $F(P)$	$MS_{Residual}$ (d.f.)
Capitula per inflorescence[b]	0.37	13.9 (0.0011)	6.7 (< 0.0001)	3.318 (447)
Florets per capitulum[b]	0.40	14.1 (0.0010)	6.7 (< 0.0001)	1579 (410)
Seeds per floret[c]	0.24	0.7 (0.40)	5.7 (< 0.0001)	0.257 (409)
Seeds per capitulum[b]	0.34	12.1 (0.0020)	5.6 (< 0.0001)	1817 (409)
Seeds per inflorescence[b]	0.40	19.1 (0.0002)	5.8 (< 0.0001)	113,278 (405)
Proportion germinated[c]	0.32	0.6 (0.43)	8.5 (< 0.0001)	0.367 (392)

[a] Population means are in Figs 3 and 4.
[b] Transformed using the Box-Cox method to meet assumptions of ANOVA (see Methods and Materials for details).
[c] Arcsine-transformed to meet assumptions of ANOVA.

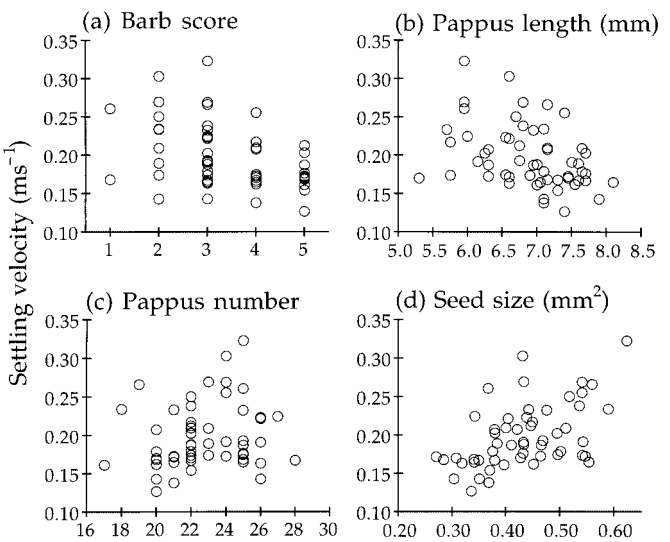


Fig. 5. Effect of four diaspore traits on seed settling velocity in *Antennaria parlinii* (n = 55 diaspores). See text and Fig. 2 for description of traits. Analysis of these data is in Table 3.

appear to have significantly higher dispersal potential, due to a combination of smaller size and larger, more heavily barbed pappus (Fig. 6). The combination of uniparental parental reproduction with high reproductive effort and seed dispersal potential has been widely observed in comparisons of outcrossing versus self-fertilizing taxa (Lloyd, 1980; Morishima *et al*., 1992). However, this is the first comprehensive investigation of reproductive trait covariation associated with the evolution of apomixis. The association between reproductive traits in *A. parlinii* also supports general predictions from life-history and

Table 3. Multiple regression[a] examining the effect of diaspore traits on settling velocity in *Antennaria parlinii*

Variable[b]	Estimated β	Standardized β	t	P
Pappus angle	–0.000652	–0.316	3.2	0.0025
Barb score	–0.00970	–0.258	2.6	0.011
Pappus length	–0.0166	–0.256	2.6	0.011
Seed size	+0.193	+0.385	3.9	0.0002

[a] For the whole model, $F_{4,49} = 15.7$, $R^2 = 0.56$, $P < 0.0001$.
[b] The four traits were not intercorrelated.

Table 4. Analysis of variance of diaspore traits and estimated settling velocity between nine sexual and 15 asexual populations of *Antennaria parlinii* with reproductive type (sexual *vs* asexual) as a fixed effect and population (nested within reproductive type) as a random effect

		Effect (d.f.)		
Variable[a]	r^2	Repro. type (1) $F(P)$	Pop'n (22) $F(P)$	$MS_{Residual}$ (d.f.)
Pappus number	0.29	0.02 (0.88)	3.9 (< 0.0001)	4.046 (213)
Barb score	0.33	18.9 (0.0002)	4.4 (< 0.0001)	0.802 (345)
Pappus length	0.39	18.8 (0.0002)	6.1 (< 0.0001)	0.257 (424)
Seed size	0.27	15.9 (0.0006)	3.7 (< 0.0001)	0.003 (424)
Settling velocity	0.56	35.8 (< 0.0001)	6.9 (< 0.0001)	0.00024 (345)

[a] Population means are in Figs 6 and 7.

metapopulation theory (Young, 1990; Olivieri and Gouyon, 1997); however, the co-evolution of all three components of reproductive strategy has not been investigated theoretically.

Presumably, the individual traits or tactics involved in a reproductive strategy become associated via natural selection. For instance, the combination of self-fertilization, high reproductive effort and enhanced seed dispersal is generally viewed as an adaptive ruderal strategy selected in ephemeral or highly disturbed habitats (Lloyd, 1980; Grime *et al*., 1988). Our comparison of basic habitat characteristics between sexual and asexual populations of *A. parlinii* is consistent with this interpretation (Table 1). Below we discuss each of our three main results in more detail.

Habitat

Our data suggest that asexual populations of *A. parlinii* tend to occur in more disturbed habitats than sexual populations (see also Asker and Jerling, 1992). In Ohio, sexual populations were more likely than asexual populations to occur in later successional, wooded habitats. Asexual populations occurred more frequently in disturbed roadside ditches and

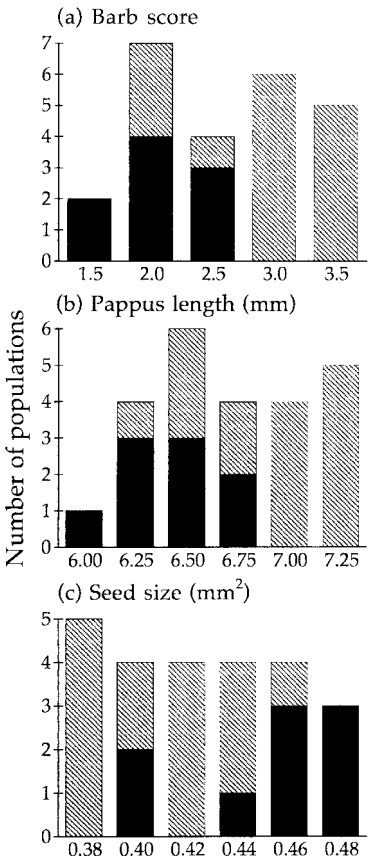


Fig. 6. Distribution of population means for potential diaspore dispersal traits for nine sexual (■) and 15 asexual (▨) populations of *Antennaria parlinii*. Summary statistics by population type are in the text. Analysis of these data is in Table 4.

fallow fields. Habitat differences were most striking in northern Ohio, where sexual and asexual populations are often located within a few kilometres. Our measures of successional stage and disturbance are crude; however, we feel that these measures have, if anything, underestimated the contrast in habitat between sexual and asexual populations. A more comprehensive comparison of habitat features (e.g. Bayer *et al.*, 1991) between sexual and asexual populations would be useful for more fully identifying the axes of habitat variation distinguishing the two reproductive types.

The results of this study agree with previous work on *A. parlinii* in Ohio. Bayer and Stebbins (1983) found that populations in the unglaciated and relatively undeveloped southern part of the state usually consist of both males and females, whereas those in the glaciated and agricultural northern region typically contain only females. Our results are also in accord with the few studies that have examined habitat differences in other species with sexual and asexual individuals (*Hieracium pilosella*, Gadella, 1987; *Poa fendleriana*, Soreng, 1986).

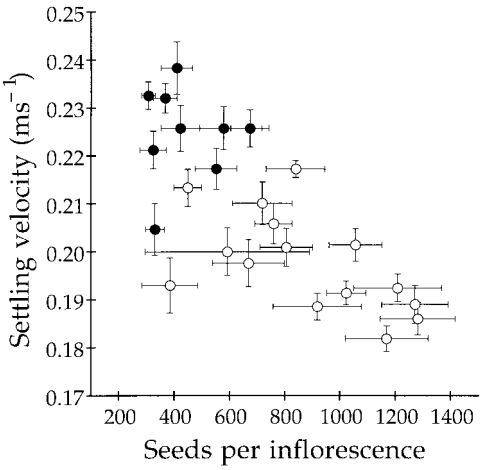


Fig. 7. Joint comparison of reproductive output (seeds per inflorescence) and seed dispersal potential (estimated seed settling velocity) between nine sexual (●) and 15 asexual (○) populations of *Antennaria parlinii*. Points are population means and error bars are ± 1 standard error. Analysis of these data is in Tables 1 and 3.

Reproductive output

Asexual ramets of *A. parlinii* produce twice as many seeds per inflorescence as sexual ramets, as a result of producing more capitula per inflorescence and more florets per capitulum (Fig. 3). Michaels and Bazzaz (1986) found a similar difference in a comparison involving three populations from Illinois. Higher seed production by asexual plants has been also found in the few other comparisons of sexual and asexual plants within species (*Antennaria parvifolia*, Bierzychudek, 1987b, 1989; *Poa fendleriana*, Soreng, 1986). These results contrast with studies on animals, which generally show that asexual species produce fewer offspring than related sexual species (Lynch, 1984). It is not known why plants and animals differ in this regard.

Among the populations of *A. parlinii* that we studied, asexual ramets may be able to produce more seed than sexual ramets because individual seeds are significantly smaller (see also Michaels and Bazzaz, 1986). However, our results do not indicate that the higher seed production by asexual plants is the result of a simple size–number trade-off. If there were a simple trade-off between seed size and number, we would expect total reproductive effort to be similar in sexual and asexual populations. However, the product of seeds per inflorescence and seed size (in mm^2) calculated at the population level is much higher for asexual populations (362.7 ± 28.5) than sexual populations (204.4 ± 21.3; $t_{22} = 3.9$, $P = 0.0008$).

If high seed production is part of an asexual reproductive strategy, then the difference in fertility between sexual and asexual plants observed in natural populations should be due to genetic differences between reproductive types rather than environmental variation associated with habitat differentiation. Our results from the greenhouse experiment support this. Asexual plants still outperform sexual plants in terms of both capitula per inflorescence and florets per capitulum when grown in a common environment.

Seed dispersal

The results of our free-fall tests suggest that wind dispersal should be greatest for small seeds with long, highly barbed pappus bristles (Fig. 5). Diaspores produced by asexual *A. parlinii* differ in the expected way from those produced by sexual plants in all of these key characteristics (Fig. 6) and, as a result, should have significantly higher dispersal potential (Fig. 7). The interpretation that these three traits are functionally linked to increase dispersal potential is further supported by the observation that pappus bristle number, the only trait that did not affect settling velocity, also did not differ between sexual and asexual populations. To our knowledge, this is the first comparison of seed dispersal potential between sexual and asexual populations.

We could not reliably assess differences in diaspore dispersal traits between sexual and asexual plants in a common greenhouse environment because large differences between reproductive types in seed set after hand-pollination (see O'Connell and Eckert, 1999) may have influenced seed size and pappus characteristics. However, it is probable that marked differences observed in natural populations are largely due to genetic rather than environmental differences. First, the difference between sexual and asexual populations in pappus characteristics and seed size were in opposite directions and thus not simply a consequence of environmental variation in factors that influence overall diaspore size. Second, as mentioned above, the only trait that did not differ between sexual and asexual populations, the number of pappus bristles, also did not affect settling velocity.

The interpretation that there is a difference in seed dispersal potential between sexual and asexual *A. parlinii* must be tempered by two important caveats. First, seed dispersal may be influenced by other traits that we have not measured in addition to seed size and pappus characteristics. When a wind-dispersed seed is released from an infructescence, the horizontal distance it will travel is likely to increase with both the height of the infructescence above the ground (Sheldon and Burrows, 1973) and the velocity of wind required to remove it from the infructescence (Greene and Johnson, 1989). Second, settling velocity measured under laboratory conditions sometimes correlates with dispersal in the field (e.g. Platt and Weiss, 1977; Augspurger and Hogan, 1983), but sometimes it does not, especially in gusty winds (Rabinowitz and Rapp, 1981; Morse and Schmitt, 1985). These considerations notwithstanding, our data are strongly suggestive of a functional association between seed dispersal potential and reproductive mode.

Adaptive differentiation in reproductive strategy

Our results support the hypothesis that sexual and asexual *A. parlinii* exhibit adaptive differences in reproductive strategy related to habitat: asexuality, high reproductive output and seed dispersal have been jointly selected to enhance persistence in disturbed habitats. Conversely, sexuality, larger seeds, reduced seed dispersal and lower reproductive effort (and presumably longer lifespan) have been jointly favoured in the more stable, wooded habitats.

Michaels (1986) and Michaels and Bazzaz (1986) reached a similar conclusion in their study of reproductive output and competitive ability involving three Illinois populations of *A. parlinii*. They suggested that habitat differentiation arises through asexual plants being excluded from sexual populations because they are unable to compete with sexual plants in stable, biotically complex habitats, presumably due to their heavier investment in seed production. In field and greenhouse experiments, the higher reproductive output of asexual

plants was associated with reduced survival and clonal propagation (Michaels and Bazzaz, 1986, 1989). When grown together in a greenhouse, sexual plants also outcompeted asexual plants (Michaels, 1986). However, it is not clear whether asexual plants are competitively excluded from wooded habitats by sexual conspecifics or they are simply not able to persist in these habitats due to other biotic or abiotic factors. In addition, the sexual plants in these experiments were uniformly tetraploid, whereas asexual plants were often hexaploid (H.J. Michaels, personal communication). Because ploidy level may affect growth rates, ecological tolerances and other life-history traits (Levin, 1983), it is not clear whether differences in survival, reproduction, competitive ability and habitat affinity observed by Michaels and Bazzaz (1986) can be generalized to populations in other parts of the geographical range where both reproductive types are almost always hexaploid (Bayer and Stebbins, 1981, 1987; Bayer, 1984). Nevertheless, their interpretation concurs well with the results of the present study.

The higher seed dispersal potential of asexual *A. parlinii* is partly due to smaller seed size. There are two complementary explanations for the difference in seed size between sexual and asexual plants: selection for smaller seeds in asexual populations to increase dispersal potential in disturbed habitats, and selection for larger seeds in sexual populations to tolerate shadier conditions in the later successional habitats (Salisbury, 1942; Westoby *et al.*, 1996; Thompson and Hodkinson, 1997). Although the difference in seed size between sexual and asexual *A. parlinii* was not associated with a difference in germination in a growth chamber environment (Fig. 4), it is possible that larger seeds enjoy higher survival in habitats typical of sexual populations.

Selection for increased competitive ability in later successional habitats may have partly contributed to the difference in seed size between sexual and asexual *A. parlinii*, but it does not explain the observation that asexual seeds had longer, more barbed pappus. Differences in pappus morphology are more likely to be the product of selection for increased seed dispersal (Sheldon and Burrows, 1973; Morse and Schmitt, 1985; Greene and Johnson, 1990). However, there are two alternative explanations for higher seed dispersal in asexual than sexual populations that do not relate to habitat disturbance. First, asexual offspring are genetically identical to both their parents and sibs and may, as a result, succumb more readily than sexual offspring to localized herbivores and pathogens (Levin, 1975; Kelley, 1994). Consequently, increased seed dispersal may be favoured in asexual populations. Second, selection may also favour increased dispersal in asexual populations so that offspring might avoid competition with genetically identical parents and sibs (Maynard Smith, 1978; Young, 1981).

Since sexual and asexual populations occur in close proximity to one another in Ohio, reciprocal transplant experiments could be used to identify more clearly the selective factors underlying the striking differentiation in reproductive strategy we have observed between sexual and asexual *A. parlinii*. More generally, comparative investigations exploiting variation in sexuality between closely related species and populations within species are required to determine whether the covariation between reproductive traits observed in *A. parlinii* reflects a general reproductive strategy in apomictic plants.

How did the strong association between reproductive mode, reproductive output, seed dispersal and habitat arise in *A. parlinii*? A simple micro-evolutionary interpretation is that divergent selection pressures in different habitats produced distinct reproductive strategies from a gene pool that varied in sexuality, reproductive output and seed dispersal (see Stebbins, 1941). This scenario presumes that asexual populations possessed sufficient

genetic variation in key reproductive traits. This may appear unlikely given the lack of recombination associated with apomixis; however, considerable recombinational variation could be supplied by even infrequent sexual reproduction (Asker and Jerling, 1992; see Bayer and Stebbins, 1983). Quantitative genetic studies comparing sexual and asexual populations would be useful for evaluating this hypothesis further.

An alternative but not mutually exclusive interpretation is that the differences in reproductive strategy and ecology between sexual and asexual populations arose at the phylogenetic inception of *A. parlinii*. *Antennaria parlinii* appears to have originated from hybridization among at least three different diploid, sexual species (Bayer and Crawford, 1986). It is conceivable that lineages arising through different sequences of hybridization might possess different combinations of traits. For example, one sequence of hybridization between diploid taxa with a preference for disturbed habitats and the associated traits may have produced apomictic lineages, while a different sequence of hybridization between woodland species gave rise to sexual lineages. In this case, trait–trait and trait–habitat associations would arise together as a direct result of hybridization. This scenario may be unlikely for *A. parlinii* because all three putative progenitor species are found in woodland habitats. Of course, hybrids may possess traits not found in their progenitor species (e.g. Bayer *et al.*, 1991). The relative contribution of phylogenetic history versus post-hybridization selection to the observed trait correlations could be assessed by using phylogenetic analysis of rapidly evolving chloroplast and/or nuclear genes to determine the origin of asexual and sexual lineages of *A. parlinii*.

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