

Patterns in plant parthenogenesis

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Summary. Plant taxa that reproduce asexually display some distinct geographical and ecological patterns. A literature review reveals that such taxa 1) tend to have larger ranges, 2) tend to range into higher latitudes, and 3) tend to range to higher elevations than do their sexual relatives. Asexual taxa have a greater tendency than sexual taxa do to colonize once-glaciated areas. These trends have previously been identified as characteristic of parthenogenetic animals as well. While many authors have interpreted these trends as providing support for the 'biotic uncertainty' hypothesis for the maintenance of sex, these trends are consistent with several other interpretations as well. Furthermore, all of these interpretations have ignored the positive correlation that exists between ploidy level and breeding system: asexual plant and animal taxa are generally polyploid, while their sexual relatives are generally diploid. Evidence is presented for plants, and by extension for animals as well, that high ploidy levels alone could (independent of breeding system) endow individuals with the ability to tolerate these 'extreme' environments. For this reason, it appears premature to interpret observed distribution patterns as evidence to support hypotheses about what forces maintain sexual reproduction. Only experimental tests, using sexuals and asexuals of comparable ploidy levels, can permit us to discriminate among the alternatives.

Key words. Apomixis; parthenogenesis; polyploidy; asexual reproduction; evolution of sex; plant breeding systems.

1. Introduction

Several recent reviews have described the ecological and geographical patterns of parthenogenesis in animals^{7,19} in an effort to determine which selective forces best explain the maintenance of sexual reproduction. These reviews conclude that parthenogenetic lineages tend to be found at higher latitudes, at higher elevations, in more xeric conditions, in more disturbed habitats, and on more island-like habitats than their sexual relatives. In general, it is argued that asexual taxa are more widely distributed than are their sexual relatives, with sexuals limited to habitats in which the important selective forces are principally biotic rather than physical.

These patterns have been explained in 4 distinct ways. First, Glesener and Tilman¹⁹ have interpreted these patterns as evidence that frequency-dependent selection, in the form of interactions with predators, parasites, pathogens, and competitors, is instrumental in maintaining sexual reproduction. Bell⁷, in an exhaustive review of animal distributions, came to a similar conclusion, as did Levin, who claimed that there existed a positive correlation between the degree of recombination engaged in by plants and the intensity of pest and pathogen pressure to which they were subjected³⁷. Secondly, other authors, especially botanists (e.g. Stebbins⁶⁰), cite the superior colonization abilities of asexual taxa as the reason for their success in marginal habitats. The third explanation was offered by Lynch, who has asserted that disjunct distribution patterns provide a prezygotic isolating mechanism that prevents parthenogens and sexuals from interfering with one another's genetic integrity, and thus producing offspring of inferior fitness. However, even when some other isolating mechanism has evolved, permitting coexistence, the range of sexual individuals is generally less extensive than that of parthenogens. Lynch's second hypothesis explained this difference as a consequence of selection on parthenogens for the acquisition of 'general-purpose' genotypes³, genotypes that are able to survive under a wide range of extreme conditions. Thus, the first hypothesis asserts that competition between sexual and parthenogenetic genotypes will cause sexuals to be dis-

placed except where sex provides an 'escape' from biotic interactions. The other 3 do not assume that such competition will necessarily occur, and attribute the observed distribution patterns to other causes: parthenogens' superior colonization abilities, avoidance of destabilizing hybridization, or parthenogens' enhanced abilities to respond to selection for general-purpose genotypes.

This paper is an attempt to evaluate these hypotheses in the light of information on the distribution patterns of asexually-reproducing plants. I have restricted myself to a consideration of plants that are apomictic in the strict sense, i.e. that produce seed mitotically, without benefit of fertilization. I hope to answer the following questions:

- 1) Are there any distinct patterns to the ecological or geographical distributions of apomictic plants?
- 2) If such patterns can be identified, is there any evidence suggesting what forces might cause those patterns?
- 3) Are there any differences, either in the patterns or in their causes, between plants and animals?

I also plan to address a potentially important issue that has received very little attention: the fact that polyploidy is an important correlate of parthenogenesis. Most asexual taxa are also polyploid taxa, and the possible influence of this factor must be considered in any explanation of distribution patterns.

2. Biology of apomixis

Many plant species are able to produce seeds asexually. While specific developmental pathways vary widely between and even within particular species, the endpoint is always the same: the embryo within these seeds is genetically identical to its maternal parent. There are two major categories of apomixis²⁴. In one, termed 'adventitious embryony', the embryo (sporophyte) arises directly from the ovular tissue of the parent, and the process of alternation of generations is completely bypassed. Rather little is known about the biology of these species, and so this review will focus on the other type of apomixis, often called 'gametophytic apomixis'. Gametophytic apomixis involves a distinct gametophytic generation, which arises either by mitosis or by a very much altered version of

meiosis in which chromosome pairing and reduction in chromosome number do not occur. The embryo develops autonomously, without fertilization. Some species of gametophytic apomicts (termed 'pseudogamous') require pollination for successful reproduction, because the endosperm must be fertilized in order to develop. In these pseudogamous species, the paternal parent makes no genetic contribution to the embryo itself. Gametophytic apomixis may be either facultative or obligate; facultative apomixis is perhaps more common¹⁰.

Gametophytic apomixis occurs most commonly among three families of angiosperms: the Compositae, the Rosaceae, and the Gramineae²⁶, but has been reported from at least 17 other families as well⁴⁸. Khokhlov³⁵ claims that apomixis has been reported in over 300 plant genera in 80 families, but these numbers are unsubstantiated; the definition of apomixis he uses is not made clear. Gametophytic apomixis is confined nearly exclusively to herbaceous and woody groups that are long-lived and cross-fertilized²⁵; annual apomicts are extremely rare. Undoubtedly this is because most gametophytic apomicts arose as allopolyploids involving the hybridization of two sexual parents, and since most annuals self-fertilize to a large extent², such hybridization is not possible.

It is almost always the case that gametophytic apomicts are polyploid while their sexual relatives are diploid⁶⁰. Undoubtedly the hybrid origin of most apomicts is a major determinant of this correlation. The same correlation between breeding system and ploidy level exists among animals^{40,42,75}. However, one difference between plants and animals is that the converse is not so often true for plants as it is for animals. Nearly all known polyploid animals reproduce parthenogenetically, while only a small fraction of the polyploid plant species are apomictic^{36,63}.

3. Distributional patterns of apomicts and sexuals

3.1 Range size

Support for the claim that apomicts have ranges that are greater than the ranges of their sexual relatives can be found among many groups of angiosperms. The quality of this support varies. Sometimes descriptions of species' ranges are very anecdotal; other times extensive collections have been made, many herbarium specimens examined, and reliable range maps constructed. Sometimes a group is well-enough known that phylogenetic relationships are reasonably clear, but in many cases this information is not available. Table 1 lists those taxa for which good distribution maps have been published, and for which an attempt has been made to determine the sexual progenitor of an apomictic line.

It is often the case that sexual species are sympatric with their apomictic relatives, and occupy an area in the center of the apomictic range; this pattern characterizes *Crepis*¹, *Parthenium*⁵², *Eupatorium*⁶⁵, and *Townsendia*⁶. Examples of the opposite trend, however, are not uncommon. Some of these are listed in table 1. More anecdotal cases include *Potentilla*, European *Antennaria*, and the genus *Cotoneaster*. *Potentilla glandulosa*, which is sexual, is 'geographically widespread'; *P. gracilis* (an apomict) is more restricted¹. The sexual species of *Antennaria* (*A. dioica*,

A. carpatica) are 'widespread'⁴⁹, while the apomicts (*A. alpina*, *A. Porsildii*, *A. Nordhageniana*) are endemic in Scandinavian mountains. Sax⁵⁴ maintains that diploid species of *Cotoneaster* (which are mostly sexual) are geographically limited relative to apomictic species, but her data provide no support for this claim: among triploids (almost certainly apomictic), 86% of 37 species have a relatively limited geographic distribution, whereas among diploids and tetraploids (most of which are sexual), 93% of 14 species have limited ranges. *Dichanthium*⁹, *Calamagrostis*²⁶, and *Sorbus*¹⁶ also appear to be exceptions to this trend. Stebbins⁶² argues that conformity with the trend is a function of the age of the species complex; only in older, 'mature' complexes will the apomicts be widespread and the sexuals rare and scattered. To evaluate whether, as a general rule, the geographic ranges of apomicts tend to exceed those of sexuals, I performed a sign test on the data in table 1. Of a total of 41 species pairs (representing 8 genera), the range of the apomictic member of the pair was greater 76% of the time. This value is significantly greater than the 50% expected by chance ($p < 0.01$).

3.2 Latitudinal trends

There is also good support for the notion that apomicts range into higher latitudes than do their sexual relatives. Again, table 1 lists only those taxa for which good distributional information is available. There are, in addition to these, more anecdotal reports. For example, Porsild⁴⁹ reports that in North America, the percentage of *Antennaria* species (Compositae) that are sexual declines with increasing latitude. The species of blackberry, *Rubus* (Rosaceae), in Sweden and Great Britain are predominantly apomictic; each country is host to only one sexual species. But in more southerly, continental Europe, there are many more sexual species²⁸. Muntzing⁴⁵ concludes that *Poa alpina* (Gramineae) in Sweden is predominantly apomictic, and points out that purely sexual strains do exist, but only in more southern countries.

A sign test comparing the ranges of the apomictic taxa in table 1 with those of their closest sexual relatives revealed that the apomictic member of the pair had the more northerly range significantly more often (76% of the time) than the 50% expected by chance ($p < 0.01$). This test included 43 species, representing 10 genera.

3.3 Elevational trends

The trend for apomicts to range further north than their sexual relatives is paralleled by an elevational trend: apomicts are often found at higher elevations than their sexual relatives. This trend is striking in *Townsendia*, the 'alpine daisy'. In *T. grandiflora*, sexual individuals are much more common than apomictic ones, but the single apomictic collection represents the highest elevational record for the species. In *T. scapigera*, apomicts are also uncommon; they occur only at or near mountain summits, despite the fact that the sexual individuals can be found at elevations anywhere from 4600 to 10,000 feet. In *T. Rothrockii*, a species in which sexuals and apomicts are equally wide-ranging geographically, the apomictic individuals are the only ones that have been observed above

10,000 feet. Apomictic *T. leptotes* are not only found over a wider geographical range than sexuals, but they tend to reach higher elevations as well. *T. condensata*, a primarily high-altitude species, is almost completely apomictic; the only sexual population known occurs on a south-facing slope, at the lowest elevation recorded for the species⁶. Another example of this tendency is provided by a pair of species in the genus *Draba* (Cruciferae). *Draba streptobrachia*, the apomictic form of the sexual *D. spectabilis*, is found only above treeline in the Colorado Rockies, while its sexual counterpart ranges from 8000 to 13,000 feet⁵⁰.

3.4 Occupancy of glaciated areas

The elevational trend just described is related to the fact that apomicts have a tendency to colonize once-glaciated areas, leaving their sexual relatives behind in the process. For example, Haskell²⁸ argues that the distribution of *Rubus* (blackberry) species in Europe (apomictic species predominate in the more northerly areas) is a consequence of glaciation, the apomicts being better able to colonize areas opened by glacial retreat. Similarly, only apomictic *Antennaria* have been collected from northeastern Canada and Greenland, which were largely glaciated⁴⁹.

Those taxa for which detailed distributional data are available are listed in table 2. I performed a chi-squared test on these data to establish whether a significant association existed between breeding system and occupancy of formerly-glaciated areas. I scored each taxon for 1) breeding system (sexual or apomictic) and 2) whether or not it ranged into areas that were once glaciated. The limits of glaciation used were as described by Flint¹⁷. This survey included 130 species (or races) in 13 genera. 75% of 57 apomictic taxa ranged into areas opened by glacial retreat, whereas only 41% of 73 sexual taxa did so; this positive association between apomixis and colonization of glaciated areas is significant ($\chi^2 = 15.35$, $p < 0.005$).

3.5 Disturbance

Several authors have tried to make the case that apomicts are found in sites that are more disturbed than those of their sexual relatives. Stebbins⁶¹ claims that the apomictic species of *Hieracium*, *Ixeris*, and *Taraxacum* are found in sites he characterizes as 'unstable' (cultivated or abandoned fields, or roadsides), while the habitats of their sexual relatives are more likely 'intermediate' (forest clearings, dry slopes, meadows, steppes) or even 'stable' (forests, swamps). Of the British Columbia species of *Hieracium*²³, the sole apomict, *H. umbellatum*, occurs in successional or disturbed habitats. Only one of the 6 sexual species grows in similar places; the others occur in stable or slowly-changing plant communities. The apomictic *Draba streptobrachia* is found on more disturbed sites (scree slopes and talus edges, where plant cover is low) than is its sexual relative *D. spectabilis*, which grows near streambanks and in moist meadows⁵⁰. The eastern North American species of *Calamagrostis* that are sexual occupy 'relatively stable, late-successional habitats', while the apomicts 'colonize disturbed, open habitats'²². Den Nijs and Sterk⁴⁶, however, found no support for this generalization in their study of *Taraxacum* in Europe. In

a test of a 1966 contention by Furnkranz that diploid (sexual) *Taraxacum* prefer relatively undisturbed sites, while polyploids (apomicts), with their higher levels of seed production, are better adapted than diploids to disturbed habitats, den Nijs and Sterk assayed the ploidy levels of plants at the same sites used by Furnkranz. They saw no evidence of obvious differences in habitats oc-

Table 1. Taxa containing both sexual and apomictic elements for which range maps or precise distribution descriptions are available. For each taxon I have noted 1) whether or not the range of the apomictic element is appreciably greater than that of the sexual, and 2) whether or not the apomictic element ranges further north than the sexual. All species are from the northern hemisphere

Taxon	Family	Apomictic range greater?	Apomictic range further north?	Ref.
<i>Arnica alpina</i>	Compositae	yes	yes	4
<i>A. amplexicaulis</i>	Compositae	yes	yes	4
<i>A. chamissonis</i>	Compositae	yes	yes	4
<i>A. lessingii</i>	Compositae	yes	no	4
<i>A. lonchophylla</i>	Compositae	yes	yes	4
<i>A. longifolia</i>	Compositae	yes	yes	4
<i>A. louiseana</i>	Compositae	yes	yes	4
<i>Bouteloua curtipendula</i>	Gramineae	no	no	20
<i>Calamagrostis lapponica</i>				
<i>C. stricta</i>	Gramineae	no	no	21
<i>C. stricta</i> ssp. <i>inexpansa</i>	Gramineae	no	no	21
<i>Crepis acuminata</i>	Compositae	no	no	1
<i>C. bakeri</i>	Compositae	yes	yes	1
<i>C. exilis</i>	Compositae	yes	yes	1
<i>C. modocensis</i>	Compositae	yes	yes	1
<i>C. monticola</i>	Compositae	yes	yes	1
<i>C. occidentalis</i>	Compositae	yes	yes	1
<i>C. pleurocarpa</i>	Compositae	yes	yes	1
<i>Eupatorium altissimum</i>	Compositae	yes	yes	65
<i>E. cuneifolium</i>	Compositae	yes	yes	65
<i>E. lechaefolium</i>	Compositae	yes	yes	65
<i>E. leucopis</i>	Compositae	yes	yes	65
<i>E. pilosum</i>	Compositae	yes	yes	65
<i>E. rotundifolium</i>	Compositae	yes	yes	65
<i>E. sessilifolium</i>	Compositae	yes	yes	65
<i>Hieracium pilosella</i>	Compositae	?	yes	70
<i>Parthenium argentatum</i>	Compositae	yes	yes	52
<i>Poa cusickii</i> ssp. <i>cusickii</i>	Gramineae	yes	yes	58
<i>P. fendleriana</i> var. <i>fendleriana</i>	Gramineae	yes	yes	58
<i>P. fendleriana</i> var. <i>longiligula</i>	Gramineae	yes	yes	58
<i>Taraxacum</i> spp.	Compositae	?	yes	46,64
<i>Townsendia condensata</i>	Compositae	yes	yes	6
<i>T. exscapa</i>	Compositae	yes	yes	6
<i>T. grandiflora</i>	Compositae	no	no	6
<i>T. hookeri</i>	Compositae	yes	yes	6
<i>T. incana</i>	Compositae	yes	yes	6
<i>T. leptotes</i>	Compositae	yes	yes	6
<i>T. montana</i>	Compositae	yes	yes	6
<i>T. Parryi</i>	Compositae	yes	yes	6
<i>T. Rothrockii</i>	Compositae	no	no	6
<i>T. scapigera</i>	Compositae	no	no	6
<i>T. spatulata</i>	Compositae	no	no	6
<i>T. strigosa</i>	Compositae	no	yes	6

cupied by the two types of individuals. The most intensively disturbed sites showed no increase in frequency of polyploid individuals in the intervening 15 years.

Another contradiction to this generalization is provided by species of *Eupatorium*, both in northeastern North America and in the Rokko Mountains of Japan. In North America⁶⁵, the habitats of the sexual and apomictic races of each species tend to be very similar, and not differentiated by degree of disturbance. For *E. altissimum*, both apomicts and sexuals are found in open woods, clearings, and alkaline prairies (though only the apomicts also grow on the ballast of railroad tracks). Both sexual and apomictic *E. lechaefolium* occupy woods and woods edges as well as old fields, fire lanes, and

highway medians. In this species, the sexual individuals are more common in the disturbed sites than in the relatively undisturbed ones, the opposite of the expected pattern. *E. rotundifolium* is found in both stable and disturbed sites, regardless of breeding system. In the Japanese species *E. chinense*, which includes both diploid sexuals and polyploid apomicts, the sexuals (which are more slender and shorter than the apomicts) cannot compete with the tall grasses and forbs found in grasslands, roadsides, and forest edges. They are restricted to scree slopes and rocky areas, which are species-poor and lack tall competitors. Thus in this case it is the sexual species, not the apomicts, that occupy the habitats that are most frequently disturbed⁷⁴.

Of 7 sexual-apomictic pairs representing 4 genera, in only 2 (29%) was the apomictic member found in more disturbed sites. In all other cases there was either no difference, or else the sexual member occupied the more disturbed areas.

Table 2. Members of groups containing both sexual and apomictic members for which information about occupancy of formerly-glaciated areas is available. For each taxon I have listed its breeding system as sexual or apomictic, and noted whether it has been collected from 1) unglaciated areas only, 2) glaciated areas only, or 3) both

Taxon	Breeding system	Family	Unglaciated only	Glaciated only	Both	Ref.
<i>Antennaria parlinnii</i>	S	Compositae			X	5
<i>A. parlinnii</i>	A	Compositae		X		5
<i>Arnica acaulis</i>	S	Compositae	X			4,76
<i>A. alpina</i>	S	Compositae		X		4
<i>A. alpina</i>	A	Compositae		X		4
<i>A. amplexicaulis</i>	S	Compositae		X		4
<i>A. amplexicaulis</i>	A	Compositae			X	4
<i>A. angustifolia</i>	S	Compositae	X			76
<i>A. angustifolia</i>	A	Compositae		X		76
<i>A. chamissoni</i>	S	Compositae		X		4
<i>A. chamissoni</i>	A	Compositae		X		4
<i>A. cordifolia</i>	A	Compositae		X		76
<i>A. diversifolia</i>	A	Compositae		X		4
<i>A. fulgens</i>	S	Compositae		X		4,76
<i>A. latifolia</i>	S	Compositae		X		76
<i>A. lessingii</i>	S	Compositae		X		4
<i>A. lessingii</i>	A	Compositae		X		4
<i>A. lonchophylla</i>	S	Compositae	X			4
<i>A. lonchophylla</i>	A	Compositae		X		4
<i>A. longiflora</i>	S	Compositae		X		4
<i>A. longiflora</i>	A	Compositae		X		4
<i>A. louiseana</i>	S	Compositae		X		4
<i>A. louiseana</i>	A	Compositae		X		4,76
<i>A. mollis</i>	A	Compositae		X		4
<i>A. montana</i>	S	Compositae	X			76
<i>A. nevadensis</i>	A	Compositae		X		76
<i>A. Parryi</i>	A	Compositae		X		4
<i>A. Rydbergi</i>	A	Compositae		X		4
<i>A. sororia</i>	S	Compositae	X			4,76
<i>A. unalaschensis</i>	S	Compositae		X		4,76
<i>Bouteloua curtipendula</i>	S	Gramineae		X		20
<i>Calamagrostis cairnii</i>	S	Gramineae	X			21
<i>C. cinnoides</i>	S	Gramineae		X		21
<i>C. deschampoides</i>	S	Gramineae		X		21
<i>C. epigejos</i>	S	Gramineae		X		21
<i>C. lapponica</i>	A	Gramineae		X		21
<i>C. pickeringii</i>	S	Gramineae		X		21
<i>C. porteri</i>	S	Gramineae	X			21
<i>C. purpurescens</i>	S	Gramineae		X		21
<i>C. purpurescens</i>	A	Gramineae		X		21
<i>C. stricta</i>	S	Gramineae		X		21
<i>C. stricta</i>	A	Gramineae		X		21
<i>Crepis acuminata</i>	S	Compositae		X		1
<i>C. acuminata</i>	A	Compositae		X		1
<i>C. bakeri</i>	S	Compositae	X			1

Taxon	Breeding system	Family	Unglaciated only	Glaciated only	Both	Ref.
<i>C. bakeri</i>	A	Compositae	X			1
<i>C. barbigerata</i>	A	Compositae	X			1
<i>C. bursifolia</i>	S	Compositae	X			1
<i>C. elegans</i>	S	Compositae			X	1
<i>C. exilis</i>	S	Compositae			X	1
<i>C. exilis</i>	A	Compositae			X	1
<i>C. intermedia</i>	A	Compositae			X	1
<i>C. modocensis</i>	S	Compositae	X			1
<i>C. modocensis</i>	A	Compositae			X	1
<i>C. monticola</i>	S	Compositae	X			1
<i>C. monticola</i>	A	Compositae	X			1
<i>C. nana</i>	S	Compositae		X		1
<i>C. nicaensis</i>	S	Compositae	X			1
<i>C. occidentalis</i>	S	Compositae	X			1
<i>C. occidentalis</i>	A	Compositae			X	1
<i>C. pleurocarpa</i>	S	Compositae	X			1
<i>C. pleurocarpa</i>	A	Compositae	X			1
<i>C. rubra</i>	S	Compositae	X			1
<i>C. runcinata</i>	S	Compositae			X	1
<i>C. setosa</i>	S	Compositae	X			1
<i>C. tectorum</i>	S	Compositae			X	1
<i>Draba spectabilis</i>	S	Cruciferae			X	50
<i>D. streptobrachia</i>	A	Cruciferae		X		50
<i>Eupatorium altissimum</i>	S	Compositae	X			65
<i>E. altissimum</i>	A	Compositae			X	65
<i>E. cuneifolium</i>	S	Compositae	X			65
<i>E. cuneifolium</i>	A	Compositae	X			65
<i>E. lechaefolium</i>	S	Compositae	X			65
<i>E. lechaefolium</i>	A	Compositae	X			65
<i>E. leucopsis</i>	S	Compositae	X			65
<i>E. leucopsis</i>	A	Compositae	X			65
<i>E. pilosum</i>	S	Compositae	X			65
<i>E. pilosum</i>	A	Compositae	X			65
<i>E. rotundifolium</i>	S	Compositae	X			65
<i>E. rotundifolium</i>	A	Compositae	X			65
<i>E. sessilifolium</i>	S	Compositae	X			65
<i>E. sessilifolium</i>	A	Compositae			X	65
<i>Hieracium pilosella</i>	S	Compositae			X	70
<i>H. pilosella</i>	A	Compositae			X	70
<i>Parthenium argentatum</i>	S	Compositae	X			52
<i>P. argentatum</i>	A	Compositae	X			52
<i>Poa alpina</i>	S	Gramineae	X			45
<i>P. alpina</i>	A	Gramineae			X	45

3.6 Other trends

I was able to find no information at all about the relative frequencies of occurrence of apomicts and sexuals on islands. However, there are a few indications that the habitat of apomicts may sometimes be more arid than that of sexuals. Sexual *Draba spectabilis* grows near streambanks and in moist meadows, while apomictic *D. streptobrachia* is found on dry scree and talus slopes⁵⁰. Sexual species of *Antennaria* (Compositae) in the Elk Mountains of Colorado are usually found in wet meadows and on the edges of ponds and streams; their apomictic counterparts occur in dry rocky meadows and on talus slopes as well (Bierzuchudek, personal observation). Of the four species of beggar's tick, *Bidens* (Compositae), in northwestern Ontario, one, *B. cernua*, is sexual, while the others (*B. frondosa*, *B. connata*, and *B. vulgata*) are apomictic. All four species are weedy annuals that grow in disturbed sites, from cracks in sidewalks to river banks,

but the sexual species is restricted to the wettest sites: beaver dams, river banks, and wet ditches¹².

4. Possible explanations for observed patterns of distribution

Most of the trends that have been identified for animal parthenogens are apparently equally valid for plants. The ranges of apomicts are larger, and often extend to higher latitudes and to higher elevations than do the ranges of their sexual counterparts; apomicts seem more tolerant of arid habitats than their sexual counterparts are. The response of apomicts to disturbance, though, is not so clear-cut; while in many groups, apomicts seem to show weedier tendencies, this behavior is not statistically significant. And little information exists on the relative frequency of apomicts and sexuals in island or island-like habitats.

Glesener and Tilman¹⁹ and Bell⁷ maintain that high latitudes, high elevations, and arid habitats all represent situations in which biological interactions are relatively unimportant. Under such circumstances, they argue, and only under such circumstances, does the greater reproductive capacity of parthenogenetic animal species confer an advantage. But in situations where competitive ability or escape from predators, parasites, and pathogens is an important prerequisite for persistence, the genetic variability that characterizes sexual progeny provides them with an advantage great enough to override their numerical disadvantage.

Other authors (e.g. Stebbins⁶⁰) cite the superior colonization ability of apomicts, their ability to found populations with a single individual, as the reason for their success in these marginal conditions, or in newly-opened habitats such as those made available by the retreat of the Pleistocene ice sheets. This explanation assumes that sexual populations could succeed in these areas once they became established, but that their establishment is extremely unlikely.

Lynch⁴² finds neither of these explanations sufficiently general. He finds the evidence for competitive inferiority on the part of parthenogens scanty and unconvincing, and rejects the colonization ability argument on the grounds that in animals, parthenogens generally have a lower reproductive rate than sexuals, and are often quite immobile; for example, most of the parthenogenetic insects are flightless⁴⁰.

The hypothesis offered by Lynch⁴² in place of these is the 'general-purpose genotype' hypothesis. Lynch suggests that obligate parthenogens are under intense selection to produce highly generalized genotypes that are able to survive under a wide variety of conditions. It is only such genotypes, he argues, that can survive extinction by environmental fluctuations. He further maintains that selection for such 'general-purpose genotypes' can be more effective in parthenogenetic populations than in corresponding sexual ones. As pointed out by Templeton⁶⁷, selection acts on the composite properties of parthenogenetic genotypes, whereas, in sexual populations, selection operates only on additive genetic variance (which apparently contributes little to tolerance of extreme environments³³). Thus, as a result of the effectiveness of this intense clonal selection, extant parthenogens have

Taxon	Breeding system	Family	Unglaci-ated only	Glaci-ated only	Both	Ref.
<i>Spiranthes casei</i>						
var. <i>casei</i>	A	Orchidaceae		X		8
<i>S. casei</i> var. <i>novaescotiae</i>	A	Orchidaceae		X		8
<i>S. cernua</i> var. <i>cernua</i>	A	Orchidaceae			X	8
<i>S. cernua</i> var. <i>odorata</i>	A	Orchidaceae	X			8
<i>S. magnicamporum</i>	A	Orchidaceae		X		8
<i>S. magnicamporum</i>	S	Orchidaceae			X	8
<i>S. ochroleuca</i>	A	Orchidaceae		X		8
<i>S. ochroleuca</i>	S	Orchidaceae			X	8
<i>Taraxacum</i> spp.	S	Compositae			X	51
<i>Taraxacum</i> spp.	A	Compositae			X	51
<i>Townsendia annua</i>	S	Compositae	X			6
<i>T. condensata</i>	S	Compositae	X			6
<i>T. condensata</i>	A	Compositae			X	6
<i>T. excinia</i>	S	Compositae	X			6
<i>T. exscapa</i>	S	Compositae	X			6
<i>T. exscapa</i>	A	Compositae			X	6
<i>T. fendleri</i>	S	Compositae	X			6
<i>T. florifer</i>	S	Compositae	X			6
<i>T. formosa</i>	S	Compositae	X			6
<i>T. glabella</i>	S	Compositae	X			6
<i>T. grandiflora</i>	S	Compositae	X			6
<i>T. hookeri</i>	S	Compositae	X			6
<i>T. hookeri</i>	A	Compositae			X	6
<i>T. incana</i>	S	Compositae	X			6
<i>T. incana</i>	A	Compositae	X			6
<i>T. leptotes</i>	S	Compositae	X			6
<i>T. leptotes</i>	A	Compositae			X	6
<i>T. mensana</i>	S	Compositae	X			6
<i>T. mexicana</i>	S	Compositae	X			6
<i>T. montana</i>	S	Compositae			X	6
<i>T. montana</i>	A	Compositae			X	6
<i>T. Parryi</i>	S	Compositae			X	6
<i>T. Parryi</i>	A	Compositae			X	6
<i>T. Rothrockii</i>	S	Compositae	X			6
<i>T. Rothrockii</i>	A	Compositae			X	6
<i>T. scapigera</i>	S	Compositae			X	6
<i>T. scapigera</i>	A	Compositae			X	6
<i>T. spathulata</i>	S	Compositae	X			6
<i>T. spathulata</i>	A	Compositae	X			6
<i>T. strigosa</i>	S	Compositae	X			6
<i>T. strigosa</i>	A	Compositae	X			6
<i>T. texensis</i>	S	Compositae	X			6

acquired the ability to be extremely generalized, which permits them to occupy a wider variety of conditions than their sexual relatives.

In the sections that follow, I will evaluate each of these hypotheses in light of the information available about the biology and distribution patterns of sexual and apomictic plant taxa.

4.1 Biotic interactions

What is the evidence that, in areas where biotic interactions are especially important, sexuals enjoy advantages over apomicts? If the genetic variability among sexual progeny provides them with advantages in certain habitats, we expect not to see coexistence between sexual and apomictic taxa in those habitats, but rather dominance by sexual lines. And certainly there are some cases in which coexistence seems to be prohibited. Sullivan⁶⁵ points out that in *Eupatorium altissimum*, *E. pilosum*, *E. rotundifolium*, and *E. sessilifolium*, all of which include both sexual and apomictic individuals, the two types never grow intermixed. Watanabe et al.⁷⁴ mention that sexual and apomictic individuals of *E. chinense* are rarely seen growing together. And the apomictic *Draba streptobrachia* is never found intermixed with its sexual counterpart, *D. spectabilis*⁵⁰. Lynch⁴² would argue that these cases can be explained equally well as the result of selection for prezygotic isolating mechanisms, to prevent destabilizing hybridization.

It is not uncommon, however, to find sexual and apomictic members of other genera growing side by side within the same 'population'. At high elevations in the Colorado Rockies, one frequently finds sites in which two or even three *Antennaria* species – some sexual, some apomictic – grow intermingled (Bierzychudek, personal observation). Bayer and Stebbins⁵ report finding sexual and apomictic individuals of *A. parlinii* in Ohio growing intermixed. In Europe, mixed populations of sexual and apomictic dandelions, *Taraxacum*, have been described by several authors^{39, 46, 64}. De Wet and Harlan¹³ report that the habitats of the apomictic grass *Dichanthium* are always simultaneously occupied by a sympatric sexual lineage.

Cases of coexistence may be more frequent than suggested by the literature, because it is often difficult to distinguish between sexual and apomictic females in the field, and mixed populations are more likely to be misinterpreted as uniform ones than vice versa. It seems quite difficult to evaluate the validity of the biotic interactions hypothesis on the basis of distributional data alone. The fact that sexuals and apomicts commonly coexist, while not sufficient to refute the hypothesis, does suggest that this explanation is perhaps too simplistic.

4.2 Colonization ability

Apomicts are seen to have two advantages over sexuals in terms of their potential to start new populations. First, they can found a breeding population with only a single colonist. Since their sexual relatives are almost always self-incompatible, the founding of a sexual population of plants requires at least two individuals that are in close proximity, and that are able to attract pollen vectors. Because of their inability to move and their requirement

of an external agent of pollen transfer, plants are more severely handicapped than animals by low population numbers. Secondly, once established, apomictic populations are expected to increase faster than sexual ones, because all their reproductive energy can be devoted to the production of female progeny. Avoiding this 'cost of producing males'⁴⁴ theoretically confers a twofold advantage. That advantage may not be as great for plants as it is for bisexual animals. Since the majority of plants are hermaphroditic, they may already be devoting more than half their reproductive energy to ovule production. For pseudogamous plants in particular, which must continue to produce pollen, there may be no differential between sexual and apomictic rates of reproduction. But while the rate of population growth may be no greater for new populations of apomictic plants, ease of establishment will undoubtedly be greater.

Lynch⁴² cites many examples of parthenogenetic animals with lower fecundities than their sexual progenitors. I am aware of no similar handicap for plants. Indeed, quite the opposite is true. In very large populations of sexual *Antennaria parvifolia* in the Colorado Rockies, rates of seed production at best equal those observed in apomictic populations of the same species. Females in small sexual populations, however (which are more the rule), rarely set as much seed as apomictic females do; pollinator service is simply not adequate to fertilize more than a small proportion of the ovules produced (Bierzychudek, unpub. data). Soreng⁵⁸ has observed a similar phenomenon in sexual and apomictic *Poa fendleriana*.

And, indeed, many observers of apomictic plants attribute their geographic distributions to their presumed greater colonizing ability: Bayer and Stebbins⁵ have done so for *Antennaria parlinii*, as have Haskell²⁸ for *Rubus*, and Catling⁸ for *Spiranthes*. To accept this hypothesis, however, we must be willing to accept a non-equilibrium view of present-day species distributions, and believe that the 'marginal' habitat occupied by apomicts but not sexuals is not intrinsically unoccupiable by sexuals, but rather that populations in these areas are subject to such high rates of turnover that at any moment they seem to be dominated by the groups capable of faster re-establishment, the apomicts. Furthermore, we must be willing to believe that the time that has passed since the retreat of the Pleistocene ice sheets has not been sufficient to permit sexuals to successfully invade the areas made available by that retreat.

4.3 General-purpose genotypes

Apomictic lines have classically been regarded as evolutionary dead-ends that possess no genetic variation and are thus incapable of response to selection⁶⁰. In order to argue that selection has acted on apomicts to produce general-purpose genotypes, it is necessary to demonstrate that apomictic populations contain genetic variability on which selection can act. There is, in fact, considerable evidence that apomictic populations contain substantial amounts of genetic variability.

Most of the documentation of this variability has focused on morphological characteristics. For example, Babcock and Stebbins¹ measured pappus length, number of florets, and length of outer bracts for 50 sexual individuals

and 55 obligately apomictic individuals of the hawkweed *Crepis acuminata*. The range of variation they observed in these characters was nearly as great among apomicts as it was among sexuals. For example, sexual plants had a mean number of florets of 7.8 ± 5.7 ; for apomicts, this value was 7.4 ± 5.6 . The difference between the two types of breeding systems was that, in the population of apomicts, most individuals were members of one of two easily recognized forms, whereas the sexual populations displayed more continuous variation.

Usberti and Jain⁷¹ grew individuals from both sexual and apomictic populations of the grass *Panicum maximum* in a randomized design under greenhouse conditions, and measured a variety of morphological and reproductive characteristics on 15 plants from each population, such as tiller number, plant height, biomass, panicle length, and days to flowering. Usberti and Jain were interested in comparing coefficients of variation in these characters for different populations, especially between sexual and apomictic populations. They detected insignificant differences in variability between the two breeding system types. Sexual populations did not show greater levels of variation; in fact, their values were exceeded by those of some of the apomictic populations. However, Usberti and Jain⁷¹ examined plants from only three sexual populations (vs. 25 apomictic ones). And since they relied on agricultural institutions for their seed, it is not clear that all the collections represent seed from the same number of individuals. However, the apomictic populations were clearly quite variable.

There are several ways in which these high levels of variability can arise within apomictic populations. Since many plants that reproduce apomictically are not obligate apomicts, but instead produce both reduced and unreduced ovules in varying proportions, both types capable of being fertilized, the progeny of these plants can be extremely genetically variable, not only in allelic composition but also in ploidy level. And even among obligate apomicts, there are several ways to generate variability. Repeated hybridization between sexual parents continues to produce new apomictic genotypes. Abnormal mitosis, especially in these high polyploids, occasionally produces an ovule with one chromosome too many or too few⁵⁹. Point mutations occur and become perpetuated. Finally, autosegregation (bivalent formation) occasionally occurs, permitting crossing-over within the parental genome.

So while to my knowledge selection experiments have never been performed on apomictic plants, most populations appear to contain a pool of genetic variation sufficient to allow such experiments to be at least partially successful. Selection acting on this pool of variability could have at least two kinds of results:

- 1) Selection could produce an apomictic 'species' that is actually a collection of distinct genotypes, each specialized for a narrow habitat, but which in sum occupy a wide range of types of environment,
- or
- 2) selection could operate to produce a 'general-purpose genotype' that can occupy an extremely wide range of habitat types.

Which of these outcomes has occurred most frequently is difficult to determine. Circumstantial evidence in support

of both scenarios exists. For example, most apomictic groups have been found to comprise a variety of genetically-distinct clones, an observation that is consistent with the first result. Turesson⁶⁹ transplanted several clones from each of many apomictic *Alchemilla vulgaris* populations into a common garden, and observed considerable variation. Hull and Groves³² report at least three morphologically distinct types of skeletonweed, *Chondrilla juncea* (Compositae) from southern Australia, where this species is an obligate apomict. Morphological differences were conserved in a common environment. Similarly, apomictic *Poa pratensis* from the Sierra Nevada consists of many different genotypes, intermingled in the same meadow¹¹. Twelve individuals sampled from near Mather and transplanted to a common environment all differed from one another with respect to one or more of these characters: habit, size, leaf color, susceptibility to disease, and flowering time. When eleven different individuals, sampled from different climatic areas, were cloned and grown under a variety of growth chamber conditions, they displayed significant differences in their growth responses to the various conditions²⁹.

Taraxacum is perhaps the best-studied example of clonal diversity; nearly 2000 'microspecies' (morphologically distinct forms) have been described⁵¹. Den Nijs et al.⁴⁷ sampled 50–100 individuals in each of many populations of apomictic *Taraxacum* in the coastal Netherlands. They found that most populations contained from 4 to 15 distinct morphotypes. Van Loenhoud and Duyts³⁹ determined that within a single site, there can be up to 20 *Taraxacum* microspecies. Laboratory germination studies demonstrated that seeds of each microspecies responded differently to light and temperature regimes, and had different responses to storage, i.e. that these morphological differences are associated with other differences that could have selective value. Ford¹⁸ showed that different *Taraxacum* clones responded in unique ways to competition with one another and with a variety of grass species.

Other studies have attempted to measure genetic variation by randomly sampling enzyme loci electrophoretically. Hancock and Wilson²⁷ sampled 3 old-field populations of *Erigeron annuus* (one of the few annual apomicts) for genetic variation at 4 enzyme loci. They identified 17 distinct genotypes. Using 6 enzyme loci, Solbrig and Simpson⁵⁷ demonstrated the presence of at least 4 distinct *Taraxacum officinale* genotypes within a 100 m² area. (*T. officinale* in North America is obligately apomictic.) No one, however, has ever done the sorts of studies that would be necessary to demonstrate that any of these clones is especially well-adapted for the particular microhabitat in which it occurs. Without such evidence, it is more reasonable to conclude that the clonal diversity we can observe within and between sites is simply a result of there being many independent sources of variability.

In support of the second proposed outcome of selection, there is evidence that some clones are in fact widespread. For example, Babcock and Stebbins¹ reported that while *Crepis acuminata* populations near the center of distribution for the species contained considerable morphological diversity, variants were much less common in more remote areas, and the same type could be found in localities that were separated by hundreds of kilometers.

Their explanation for this phenomenon was, first, that the source of new variants is repeated hybridization between sexual parents, so variants will be more common nearer sexual populations, and, second, that apomictic clones on the margins of the range will have been subjected to more intense selection, because their environments are more extreme.

Perhaps the best evidence for the existence of widespread genotypes comes from a study by Lyman and Ellstrand⁴¹, who surveyed 22 North American populations of *Taraxacum officinale* for variation at 5 enzyme loci. They used the phenotypic trait of seed color to further resolve differences. By these methods they demonstrated that their sample of 518 individuals included at least 47 distinct genotypes. The average number of genotypes per population was 5. Most clones (66%) were found in only one population, but a few were extremely widespread. One, for example, was found in 19 populations ranging from Vermont to California to Alaska. If this is indeed a single clone (and not a heterogeneous group, among which genetic variation existed but was not detected), it certainly seems to have the potential to be a general-purpose genotype. But a general-purpose genotype is widespread, in theory, because of a broad physiological tolerance, and we have no information on the fitness of these plants under different environmental conditions; so far, then, these few examples provide only very weak support for the idea of general-purpose genotypes as a general explanation for observed distribution patterns.

5. Polyploidy and distribution patterns

When trying to construct an explanation for the distribution patterns of apomicts or parthenogens relative to sexuals, it is important to recognize that a striking correlate of asexual reproduction among both plants and animals is polyploidy. Recent observers of distributional trends among animals^{7,19} have ignored this correlation, and have attributed the causes of those patterns to breeding system differences rather than to ploidy level differences. Because there are very few sexual polyploids among animals, deconfounding the two possible causal factors is quite difficult. However, polyploidy is extremely common among sexually-reproducing plants, a fact that makes it possible to examine whether polyploidy alone might not provide an adequate explanation for the observed differences in distribution patterns between sexuals, which are generally diploid, and apomicts, which are nearly always polyploid. The evidence that polyploidy alone endows plants with characteristics that could influence their distribution patterns is in fact quite persuasive.

Long before evolutionary biologists began to notice the phenomenon of geographical parthenogenesis, botanists were drawing attention to the fact that, in flowering plants, the frequency of polyploids tends to increase with increasing latitudes, and often increases with increasing elevation¹³. Disclaimers have been made that such surveys in the past have failed to recognize that the frequency of plant growth-forms also varies with latitude (frequency of perennials increases at higher latitudes), and that since ploidy levels are correlated with growth form (perennials are more likely to be polyploid than

annuals are), this trend is not as striking as it first appears¹⁵. However, an examination within taxonomic groups and within geographic areas still reveals the existence of these trends:

- 1) Diploids are often more limited in distribution than are their tetraploid relatives^{36, 53, 62}.
- 2) High polyploids often occur in upper alpine sites³⁶.
- 3) Polyploids demonstrate a marked tendency to successfully colonize once-glaciated areas, while their diploid progenitors remain in unglaciated places, and are often limited to refugia^{15, 34, 36, 43, 60}.

The explanation most often offered to account for these observations has been a genetic one, an argument that rests on the genetic variability presumed to characterize polyploids as a result of their hybrid origin. Polyploids often arise from the fertilization of an accidentally unreduced diploid female gamete from one individual by a normal haploid male gamete from another. The triploid organism that results may produce unreduced triploid female gametes that are then fertilized by haploid male gametes to form tetraploid offspring¹³. Thus the genotype of many polyploids may contain complete or partial genomes from as many as three genetically distinct individuals. This condition can confer several advantages: 1) The multiple copies of genes so acquired can provide pathways for the development of new gene functions, and 2) by combining the genetic information of several individuals, offspring can be produced that have more physiological and ecological flexibility than any of their parents; polyploids so produced may be expected to be more heterozygous than any of their parents⁵³. Indeed, since polyploids must originate sympatrically with their progenitors, their widespread success attests to the fact that at least some of the polyploids that are produced must be as fit or more fit than the genotypes that produced them⁵⁵.

A variety of experiments has demonstrated that hybrids, and thus polyploids, can display a wider range of tolerance than their ancestors. For example, when Hiesey and Nobs³⁰ produced hybrids between different ecological races of *Achillea millefolium*, some of the F₁ and F₂ progeny had ecological tolerances exceeding those of either parent. In a later study, Hiesey and Nobs³¹ crossed two different species of *Poa*, both of which were facultatively apomictic, then transplanted twelve lines of apomictic F₂ progeny to three different environments, along with their parents. One of the progeny lines outperformed both parents at all three transplant stations. Smith⁵⁶ performed a comparison of the physiological and morphological characteristics of different chromosomal 'races' of *Sedum pulchellum*. She found, by growing plants in a common environment, that the hexaploids were more tolerant of extremes of soil moisture than were diploids, and that the competitive ability of seedlings increased with ploidy levels. This was true regardless of whether seedlings were competing with individuals of the same ploidy level or of different ploidy levels. Tal⁶⁶ compared the response of diploid and tetraploid plants of cultivated tomato (these were autotetraploids, so they did not have the advantage of possessing two genomes) to salinity stress, and found the tetraploids to be more tolerant of salinity than the diploids. Tomkins and Grant⁶⁸, who examined a variety of morphological and genetic factors for their ability to

predict the response of 75 weed species to herbicides, found that the ploidy level of plants resistant to herbicides was significantly higher than the ploidy level of susceptible plants.

Finally, in a recent review of the role of polyploids in generating evolutionary novelty, Levin³⁸ cites a number of examples of polyploid plants that are more resistant to pathogens and pests, or more tolerant of low nutrients, or more drought or cold resistant, than their diploid progenitors.

6. Conclusions

The differences in distribution patterns between sexuals and parthenogens have been recognized at least since 1928, when Vandell⁷² coined the term 'geographic parthenogenesis' for this phenomenon. The recent resurgence of interest in the evolution of sexual reproduction has seen this pattern cited as support for the hypothesis that sexuality is favored by biotic selection. However, proponents of this view have failed to note the correlation between breeding system and ploidy level that characterizes both plants and animals, and have ignored the potential confounding influence of polyploidy. Vandell⁷³ himself drew attention to the correlation between polyploidy and parthenogenesis, and observed that it was possible in plants (though difficult in animals) to separate the two effects, so this observation is not original. However, in light of the attention being received by the 'biotic selection' explanation for the maintenance of sex, it seems important to point out that occupancy by parthenogens of wider ranges and more extreme conditions is just as likely to be the consequence of their high ploidy levels as of their breeding system; in fact, this appears to be the more parsimonious conclusion. It seems premature, then, to interpret the trends identified in this paper and by Glesener and Tilman¹⁹ and Bell⁷ as support for the biotic interaction hypothesis, or for any other hypothesis; because of the confounding of breeding system and ploidy level, proper testing of alternative hypotheses must be done by experimental studies in which ploidy level is held constant.

It also seems important to point out that the 'biotic interaction' explanation for these patterns rests on a completely untested assumption: that in areas of co-occurrence, parthenogens will experience intense competition with their sexual progenitors, who will not succeed unless their numerical disadvantage is countered by some corresponding advantage. It seems equally likely that the two forms will have quite different ecological properties, and are no more likely to be ecologically identical than any two congeners are. Indeed, it is hard to believe that the observed cases of coexistence between sexuals and parthenogens described in this paper are cases in which the competitive abilities of the two are exactly equal. Rather, it seems probable that the two forms are sufficiently ecologically distinct to coexist. If we do not assume that sexuals and parthenogens necessarily compete where they co-occur, then the phenomenon of geographical parthenogenesis is consistent with two other hypotheses: 1) that the greater range of parthenogens is a product of their greater potential for establishing new populations, and 2) that parthenogens are the product of selection for

general-purpose genotypes. Descriptive studies alone will not permit us to distinguish among these hypotheses.

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