

THE DYNAMIC NATURE OF APOMIXIS IN THE ANGIOSPERMS

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Apomixis, the asexual production of seed, is a trait estimated to occur in fewer than 1% of flowering plant species, with an uneven distribution among lineages. In the past decade, targeted research efforts have aimed at clarifying the genetic basis of apomixis, with the goal of engineering or breeding apomictic crops. Recent work suggests a simple genetic basis for apomixis, but it also indicates that natural populations of apomicts are much more complex than is often assumed. For example, in nature, nearly all apomicts that go through a megagametophyte stage (gametophytic apomicts) are polyploid, while their sexual relatives are typically diploid. Although populations have been characterized as obligately sexual or apomictic, it is increasingly clear that many plant populations exhibit some variation in reproductive mode. Many apomicts retain residual sexual function as pollen donors and thus have the potential to spread apomixis via male gametes, thereby increasing the genetic diversity observed within apomictic populations. Here, we summarize our current understanding of the genetic basis and transmission of apomixis. We use insights from previous case studies and models for the spread of asexuality to explore the potential for establishment and spread of apomixis in nature.

Keywords: apomixis, asexual reproduction, cost of sex, *Crepis*, polyploidy.

Introduction

Sexual reproduction is a nearly universal characteristic of angiosperms. Despite the overwhelming importance and broad occurrence of sexuality, most plant species (other than annuals) are capable of some form of asexual propagation, though in the majority of cases, this remains an augmentation to sexual reproduction rather than the dominant reproductive mode (Richards 2003; Silvertown 2008). In a number of groups, however, asexuality has become predominant through evolutionary transitions from sexuality. Whereas some plants have evolved asexuality through the degeneration of sexual structures in favor of vegetative means of propagation (Eckert 2002; Silvertown 2008), the more common route to asexuality is through the evolution of apomixis, the production of clonal seed in the absence of fertilization (Richards 1986). First described by Smith (1841), apomixis is now reported in more than 300 species in more than 40 angiosperm families (Asker and Jerling 1992). Thus, evolutionary transitions to asexual reproduction have occurred repeatedly in flowering plants, with only rare shifts in the reverse direction (Chapman et al. 2003).

Asexual reproduction in plants has received steady attention from ecologists and evolutionary biologists during the past several decades, including summaries in classic works by Stebbins (1950), Harper (1977), Grant (1981), and Richards (1986), among many others. In recent years, significant attention has been given to determining the genetic basis of apomixis (reviews in Grimanelli et al. 2001; Ozias-Akins 2006), with an eye to the development of apomictic crops. Another area of active research focuses on understanding natural variation in

apomictic complexes, notably in *Taraxacum* (van der Hulst et al. 2000; Verduijn et al. 2004; Meirmans et al. 2006), *Hieracium* (Gadella 1987; Bicknell et al. 2003; Houliston and Chapman 2004), and *Crataegus* (Muniyama and Phipps 1979a, 1979b, 1984a, 1984b; Dickinson and Phipps 1986; Talent and Dickinson 2005, 2007). Here, we focus on the genetic, population genetic, and ecological factors that affect the dynamics of establishment and spread of asexual lineages. We are especially interested in the contributions of occasional sexual reproduction to the establishment and spread of asexuality and specifically in the role that pollen plays in this context. Maynard Smith (1978, p. 66) noted the potential importance of pollen in the spread of apomixis, but this area remained largely unexplored before work by Mogie (1992). Since this time, substantial insights into the spread of apomixis have been gleaned from theoretical and empirical work, and we summarize these findings and identify areas for future work.

A Brief Description of Apomictic Phenomena

Throughout this review, “apomixis” is used synonymously with “agamospermy” (Stebbins 1950), referring to the asexual production of seed. Other terms describing apomixis are defined in table 1. Apomixis is unknown in gymnosperms, although cleavage polyembryony, the cloning or twinning of embryos from the same sexual zygote, is well documented (Mogie 1992). The pathways by which apomictic seeds are produced are divided into three broad categories (table 1; Stebbins 1950): adventitious embryony, diplospory, and apospory. The latter two categories are referred to collectively as gametophytic apomixis (Stebbins 1950; Grant 1981; Asker and Jerling 1992). In each case, apomictic embryos are derived from maternal genetic

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Table 1
Description of Apomictic Phenomena in Flowering Plants

Mode of apomixis	Origin of embryo	Endosperm development	Ploidy	Pollen	Genetic basis	Frequency of apomictic seeds	Taxa
Adventitious embryony	Somatic tissue surrounding ovule; sexual ovule must be fertilized	Requires development of sexually fertilized seed	Usually diploid	Necessary for sexual reproduction	Little studied; one locus dominant?	??	Widely distributed, especially Rutaceae, Celastraceae, and Orchidaceae
Gametophytic apomixis: Diplospory	Unreduced megaspore mother cell gives rise to unreduced megagametophyte	Usually autonomous	Rarely diploid	May transmit apomixis	Two unlinked loci	High	Asteraceae
Apospory	Nucellus gives rise to unreduced megagametophyte	Usually pseudogamous	Rarely diploid	Necessary for endosperm development	Single linkage block; 1+ dominant loci	High	Poaceae and Rosaceae

material, but each is associated with different probabilities of producing sexual progeny, different selection pressures to maintain male fertility, and, consequently, different expected levels of genetic diversity within populations.

In adventitious embryony, embryos develop from somatic cells (either from the nucellus or from the integument of the ovule) rather than from the megagametophyte. In gametophytic apomixis, unreduced megagametophytes are produced that subsequently develop into embryos. In this case, the cell that gives rise to the megagametophyte can have one of two origins. In diplospory, the unreduced megagametophyte is produced by the modification or circumvention of meiosis in the megaspore mother cell—the same cell that would give rise to sexual megagametophytes. In apospory, the unreduced megagametophyte arises through mitotic divisions of a cell of the nucellus, usually in conjunction with or following degeneration of the sexual megagametophyte. Diplospory and apospory describe the processes generating the mature megagametophyte; apomixis results when the unfertilized egg undergoes parthenogenetic development to produce the embryo.

Some apomicts require pollen for proper seed maturation (the alternative is called autonomous apomixis; Nygren 1967). In most of these cases, pollen is necessary for the proper development of the endosperm, with at least one of the pollen nuclei fusing with at least one of the polar nuclei of the megagametophyte (Richards 1986). This phenomenon is known as pseudogamy. Adventitious embryony is usually pseudogamous. Among gametophytic apomicts, pseudogamy is prevalent among aposporous apomicts, whereas autonomous endosperm formation is more common with diplospory (Richards 1986). The requirement for fertilization of the endosperm selects for the maintenance of at least some viable pollen (Noirot et al. 1997). Apomicts with autonomous endosperm formation tend to produce less viable pollen and, in some cases, are male sterile (Meirmans et al. 2006; Thompson and Whitton 2006; Thompson et al. 2008). In rare cases, apomicts have been shown to require pollination to stimulate seed development, even though neither the embryo nor the endosperm is fertil-

ized (Bicknell et al. 2003). In the following, we describe the major classes of apomicts in more detail and discuss the implications of each for pollen maintenance and for the production of mixtures of sexual and asexual seed.

Adventitious Embryony

Unlike gametophytic apomixis, adventitious embryony has the potential to occur in parallel with sexual megagametophyte development (Nygren 1967; Asker and Jerling 1992). In most cases that have been examined, the sexual embryo sac appears to develop normally, and pollination followed by double fertilization initiates both sexual embryo and endosperm development. Once the sexual embryo is initiated, additional somatic embryos develop from cells of the nucellus or the integuments (Naumova 1993). A large proportion of taxa with adventitious embryony can produce multiple embryos per seed (polyembryony), one of which may be sexual (Richards 2003). In some cases, these embryos have been shown to compete for the resources of the endosperm (Grant 1981; Naumova 1993), with the percentage of asexual seed varying according to the outcome of the competition. The relative success of sexual versus asexual embryos therefore varies among species and conditions. For example, the percentage of asexual seed ranges from 33% in Eureka lemon to 100% in Dancy mandarin among *Citrus* cultivars (Reuther et al. 1968, in Grant 1981).

Numerous embryological observations of at least occasional adventitious embryony led some authors to conclude that this is the most taxonomically widespread form of apomixis (Naumova 1993; Carman 1997), despite being the least well known in terms of both its importance in nature and the genetic basis of apomixis. With the occurrence of sexual and asexual processes alongside each other, parallels are often drawn between adventitious embryony and vegetative reproduction because asexuality is often facultative in both cases (Grant 1981; Nogler 1984). It is unclear whether this is a fair representation, however, because so little is known about the frequency of asexual seed production in taxa with adventitious

embryony. Furthermore, the phenomena of adventitious apomixis and vegetative reproduction have very different implications for dispersal and for the production of seeds capable of surviving inhospitable seasons (Richards 2003).

Another interesting feature of adventitious apomicts is that they are frequently diploid (or of the same ploidy as their sexual relatives), a situation that is exceedingly rare among gametophytic apomicts (Asker and Jerling 1992; Koltunow 1993). That so little is known about the population biology of adventitious embryony (Naumova 1993) limits our ability to draw inferences about this phenomenon.

Gametophytic Apomixis

The two forms of gametophytic apomixis, apospory and diplospory, have been studied in far greater depth than adventitious embryony and are better understood (Richards 1986; Mogie 1992). Among the most striking features of gametophytic apomixis is its strong correlation with polyploidy: of examples in more than 126 genera (Carman 1997), less than a handful are reported to include diploids (Nogler 1984; Mogie 1992; Schranz et al. 2006), and some of these cases are not supported by recent studies (e.g., *Potentilla argentea*; Holm et al. 1997). Whereas odd ploidy levels (e.g., triploidy, pentaploidy) are often reliable predictors of the presence of apomixis, tetraploidy is the most common ploidy level among apomicts (Asker and Jerling 1992). Explanations for the association between gametophytic apomixis and polyploidy are numerous and varied; they include mechanisms that focus on the ecology of polyploids and apomicts (Stebbins 1950), the genetic consequences of polyploidy and apomixis (Lokki 1976; Manning and Dickson 1986), the genetic basis of apomixis (Mogie 1992), and the shared role of unreduced gamete formation (Harlan and deWet 1975). We return to this association in “What Is the Genetic Basis of Apomixis?”

Diplospory

Diplosporous embryos are the product of either a complete omission of meiosis or an abnormal meiosis that yields unreduced products, one of which develops mitotically into the unreduced megagametophyte. Because diplosporous megagametophytes are derived from the megaspore mother cell, diplospory interferes directly with sexual reproduction, and thus individuals exhibiting diplospory are more likely to be obligately asexual, assuming that whatever is interfering with normal meiosis is expressed uniformly in all ovules. Diplospory can lead to genetically variable offspring if crossing over or automixis (Thompson and Ritland 2006) occurs before the cessation of meiosis.

Apospory

In aposporous apomicts, the unreduced megagametophyte is derived from a somatic cell of the ovule (rather than the megaspore mother cell), which undergoes mitotic divisions to form a megagametophyte. Meiosis in the megaspore mother cell usually appears normal, but products may begin to degenerate soon after meiosis is completed (Albertini et al. 2001). Aposporous apomicts have been shown to produce some sexual offspring through fertilization of reduced and unreduced megagameto-

phytes (Bicknell et al. 2003). In some cases, however, even if mature sexual embryo sacs are produced and the aposporous initials fail to develop, sexual embryos may not be viable (Nogler 1984). Whether this represents anomalies in sexual development that contributed to the selective advantage of apomixis or reflects a breakdown in sexual reproduction that occurred after apomixis arose is unknown.

The distinction between apospory and diplospory is not as sharp as the previous descriptions would suggest. This is best illustrated in the Rosaceae, where apospory and diplospory have been described in the same individuals (Muniyamma and Phipps 1984a). This intriguing observation may arise from the difficulty of distinguishing somatic and generative cells in the multicellular female archesporium (the part of the nucellus that gives rise to the megaspore mother cell) of many Rosaceae (Asker 1980). However, there are several species in which both diplospory and apospory occur, leading some workers to speculate that these two modes of megagametophyte formation share a common genetic basis (Mogie 1992).

Taxonomic Occurrence of Apomixis

Apomixis occurs sporadically among the ca. 457 angiosperm families (APG 2003). Carman (1997) lists more than 330 genera with apomixis, with more than two-thirds of these being taxa with adventitious embryony. The frequency of asexual reproduction in taxa reported to produce adventitious embryos is poorly documented; thus, this number provides less information about the importance of asexuality in nature than do the numbers for gametophytic apomicts. Of ca. 126 genera known to include gametophytic apomicts (Carman 1997), roughly three-fourths of cases occur in just three families—the Rosaceae, Poaceae, and Asteraceae, which together comprise ca. 15% of angiosperm species (Richards 1986; Asker and Jerling 1992; APG 2003). Estimating the total number of apomictic species is inherently problematic because of the wide differences of opinion on the taxonomic treatment of apomicts (Richards 2003), but it is unlikely that more than 1% of flowering plant species are substantially apomictic. Predominant mechanisms of apomixis also differ among taxonomic groups: members of the Rosaceae and Poaceae are most often aposporous, whereas apomictic Asteraceae are commonly diplosporous (table 1). Reports of adventitious embryony are rare in these three families (Asker and Jerling 1992; Naumova 1993). Adventitious embryony is most frequent in the Rutaceae, Celastraceae, and Orchidaceae (Naumova 1993). Although adventitious embryony is most common in tropical or subtropical trees and shrubs, gametophytic apomixis is described as most common in temperate perennial herbs (Asker and Jerling 1992). However, no surveys of apomixis to date correct for possible correlations between taxonomy and growth forms or geographic distribution.

Regardless of the precise numbers, the broad taxonomic distribution indicates that apomixis, in all of its various forms, has arisen multiple times. It also suggests that the different forms of apomixis either are more likely to arise or are more likely to establish in some groups than in others. What might account for such patterns? Different explanations have been offered for the distribution of different forms of apomixis. For example, it has recently been observed that pollen limitation is

more severe in tropical taxa, especially among self-incompatible species and trees (Vamosi et al. 2006), which might selectively favor adventitious embryony as a strategy to augment reproductive output. However, the taxonomic distribution of apomixis may be determined by appropriate genetic opportunities rather than being favored by ecological circumstances. Members of the Rosaceae, Poaceae, and Asteraceae have been shown to produce high frequencies of unreduced gametes, especially in hybrids (Ramsey and Schemske 1998, their supplementary table 1), which might provide repeated opportunities for the evolution of gametophytic apomixis. However, the same is true of other taxa (e.g., Liliaceae, Convolvulaceae) in which apomixis is not particularly common. Further study is necessary to confirm—or refute—these hypotheses.

What Is the Genetic Basis of Apomixis?

The promise and prospect of harnessing apomixis as a tool for use in agriculture and plant breeding have resulted in the proliferation of studies aimed at identifying genes that contribute to the control of apomixis, with apomictic grasses thus far receiving the most attention (Ozias-Akins 2006). Most genetic studies rely on the production of meiotically reduced viable pollen in apomicts to study segregation of the trait in F₁ progeny from crosses with sexually reproducing female parents. A number of excellent reviews provide detailed summaries of the genetics of apomixis (Grimanelli et al. 2001; Grossniklaus et al. 2001; Ozias-Akins 2006). As in these works, we focus here on more recent studies using molecular genetic approaches.

The genetic basis of adventitious embryony has apparently been studied only in *Citrus* (Garcia et al. 1999). In this case, the 3 : 1 ratio of apomictic to sexual offspring suggests the action of a single locus, with the apomixis allele being dominant. However, quantitative trait locus (QTL) analysis identifies at least three independently segregating markers that appear to be associated with apomixis in this system, with additional loci involved in the control of polyembryony. The QTL analysis relied on relatively few markers (69) and progeny (50), and so these conclusions are somewhat preliminary.

Gametophytic apomixis is typically dissected into two traits, which potentially have different genetic bases: unreduced megagametophyte formation (through apospory or diplospory) and parthenogenetic development of the embryo. In the case of autonomous apomixis, proper endosperm development without fertilization represents a third genetic change required for apomixis. Studies of the genetic basis of apospory in seven species (Poaceae: *Pennisetum squamulatum*, *Pennisetum ciliare*, *Panicum maximum*, *Brachiaria* sp., *Paspalum notatum*; Ranunculaceae: *Ranunculus* sp.; Asteraceae: *Hieracium* sp.) have found that aposporous megagametophyte development and parthenogenesis cosegregate as a single dominant locus (see references in Ozias-Akins 2006). Some of these studies have shown that the region controlling aposporous apomixis has reduced recombination, with multiple markers and potentially multiple genes falling within the linkage group (Ozias-Akins 2006). The only clear example of segregation of apospory from parthenogenesis is in *Poa pratensis* (Albertini et al. 2001; Matzk et al. 2004). In this case, whereas apospory and parthenogenesis

cosegregated in the majority of progeny, two individuals showed signs of apospory without parthenogenesis, supporting the idea that at least two loci inherited as a single linkage block control aposporous apomixis.

The genetic control of diplosporous apomixis is well studied in three systems: *Erigeron* and *Taraxacum* in the Asteraceae and *Tripsacum* in the Poaceae (Ozias-Akins 2006). In two of these cases, control of apomixis involves two unlinked loci separately controlling the production of diplosporous megagametophytes and their parthenogenetic development (van Dijk et al. 1999; Noyes and Rieseberg 2000; Noyes et al. 2007). In *Tripsacum*, although the two components of apomixis appear to co-occur on a single linkage group, recombination between them has been detected (Grimanelli et al. 1988). However, only in recent work in *Erigeron* (Noyes et al. 2007) does recombination appear to occur freely, with nearly equal proportions of the four expected phenotypic combinations from a cross between a sexual seed parent and an apomict-sexual hybrid.

Interesting trends emerge from the genetic data obtained thus far. First, the evidence consistently suggests that most of the alleles controlling apomixis are dominant. This may not be surprising, given the association between apomixis and polyploidy, which, in a tetraploid, would require four copies of recessive alleles to be expressed. Mechanistically, dominance suggests that apomixis involves an active trigger of adventitious embryony, unreduced gamete formation, and parthenogenesis rather than inactivating mutations that knock out normal functions, which tend to be recessive. This is contrary to the views of Grimanelli et al. (2001), who suggest that apomixis arises as a deregulation of sexual function.

A puzzle about the genetics of apomixis raised by Asker (1980) and others is the requirement for nearly simultaneous transitions in the formation of megagametophytes and in embryo development. The chance that two mutations causing these two shifts would occur soon after each other within a small nascent apomictic population seems prohibitive; yet, without the simultaneous emergence of the two traits, apomixis seems unlikely. For example, the development of functional diplosporous megagametophytes without parthenogenesis would lead to embryos with increasing ploidy in each generation, whereas the converse would produce haploids. This puzzle led Asker and Jerling (1992) to argue in favor of a single-gene mechanism, with one mutation causing both unreduced egg formation and parthenogenesis. To date, however, several studies (cited previously) implicate multiple loci, whereas no study has yet to demonstrate that only a single gene is involved (although this may turn out to be the case in some of the examples involving a single linkage group). One way around this puzzle is suggested by the observation that parthenogenesis may be triggered by the presence of unreduced megagametophytes, at least to some extent. Among the segregants of *Erigeron* examined by Noyes and Rieseberg (2000), offspring inheriting the parthenogenesis alleles did not express the trait unless diplospory was also present, a possibility also suggested by the work of Albertini et al. (2001) in *P. pratensis*. However, the most recent work on *Erigeron* (Noyes et al. 2007) has found autonomous development of embryos and endosperm in *Erigeron* without diplospory; aneuploidy may be responsible for the incomplete penetrance observed in the earlier work. Even so, parthenogenesis was more extensive when diplospory was also

present. These studies suggest that it is possible that a sexual diploid could harbor alleles for parthenogenesis with little to no penetrance and that the expression of such alleles could increase once unreduced ovules are produced.

Another possible route to the coestablishment of unreduced embryo production and parthenogenesis is through hybridization, a long-recognized correlate of apomixis (Stebbins 1950; Asker and Jerling 1992). In a number of examples, hybrids produce a much higher frequency of unreduced gametes than do their parents (Ramsey and Schemske 1998, their supplementary table 1), with frequencies reaching 86%. This suggests that meiosis is deregulated to some extent in newly formed hybrids, leading to an automatic increase in unreduced gametes. Simultaneously, parthenogenesis might be favored in hybrids to avoid the production of lower-fitness F_2 offspring resulting from genetic incompatibilities. If unreduced gamete formation in hybrids leads to triploid formation, then later-generation hybrids could also have decreased fitness due to segregation problems, further favoring parthenogenesis. In addition, recurrent hybridization also provides a continual supply of individuals of different genetic constitutions, increasing the chance that a lineage capable of both unreduced gamete formation and parthenogenesis arises.

Another observation of interest is that the alleles or linkage blocks contributing to apomixis are, at least in some cases, lethal in haploid pollen (Nogler 1984; Roche et al. 2001). Because gametophytic apomixis is typically associated with regular meiosis in pollen (Mogie 1992; see recent examples in Bicknell et al. 2003; Noyes et al. 2007; Talent and Dickinson 2007), diploid carriers would be unable to pass such alleles to their offspring through pollen. This suggests that the mutations leading to apomixis likely established in lineages either that had previously become polyploid (so that the mutant allele gained fitness through pollen) or that were predisposed to parthenogenetic development (so that the mutant allele gained fitness through apomictic seeds). This assumes that haploid lethality is associated with apomixis from the beginning. Alternatively, haploid pollen of apomicts might be viable initially and then might gradually deteriorate due to the relaxation of selection pressure on pollen.

The Expression of Apomixis in Polyploids

These findings also shed some light on the association between gametophytic apomixis and polyploidy. Because the formation of unreduced megagametophytes is a characteristic feature of gametophytic apomicts, as well as a key element in the production of polyploids in sexuals (Harlan and deWet 1975; Ramsey and Schemske 1998), it is tempting to infer that unreduced egg formation is the causal link between apomixis and polyploidy. However, whether this is the causal link and exactly how it might work remain unclear.

One possibility is that a mutation causing a high frequency of unreduced gametes first becomes established within a sexual population, generating a high frequency of polyploids but also selecting for parthenogenetic development to avoid low-fitness offspring of even higher ploidy levels. However, one problem with this model is that it is difficult to explain how a mutation generating a high frequency of unreduced gam-

etes would survive for long within a sexual population. In a sexual diploid, not only would such a mutation generate a high frequency of triploid offspring, but also pollen fitness would be severely reduced if alleles for the production of unreduced megagametophytes are lethal in haploid gametes (Nogler 1984; Roche et al. 2001).

Another possible causal link between unreduced gametes and polyploidy assumes that apomixis first becomes established in diploids by a simultaneous increase in the frequency of unreduced gametes and parthenogenesis (as discussed previously). In such a nascent apomictic population, occasional fertilization of unreduced eggs may occur, generating higher ploidy levels until such time that stricter mechanisms to avoid fertilization have evolved, which would produce the association between apomixis and polyploidy as well as patterns of multiple ploidy levels observed in many apomictic groups. Although this model does not preclude the persistence of diploid apomicts, one would predict that ploidy levels would rise by a ratchet mechanism (Meyers and Levin 2006) if increases in ploidy are much more common than reductions. Indeed, the modeling results of Meyers and Levin (2006) suggest that because of the irreversibility of increases in ploidy level, polyploids can achieve high frequencies within lineages over time even if they are at a selective disadvantage. In a system with apomixis, diploid apomicts would be subject to stochastic loss, with little possibility of replenishment through ploidy reduction. In addition, any factor that limited the persistence or spread of apomixis genes in diploids would accentuate this pattern.

It remains possible, however, that the link between polyploidy and apomixis is not causally related to unreduced gamete formation. Rather, apomixis and polyploidy might be induced by yet another factor. For example, both apomixis and polyploidization could be selectively favored in hybrids between two species as mechanisms to avoid hybrid breakdown and to ensure balanced segregation of parental genomes. Such polyploids, originating from crosses between different species, are known as allopolyploids, whereas those polyploids originating within one species are termed autopolyploids. Autopolyploidy has traditionally been thought to contribute rarely to long-lasting polyploid lineages, but this has recently been called into question. Soltis et al. (2007) point out several cases in which autopolyploid origins are more parsimonious. Determining whether there is a bias toward allopolyploidy among apomicts will help to shed light on the causal mechanisms linking apomixis and polyploidy. If most apomicts are allopolyploid, we would infer that hybridization is the key causal link between apomixis and polyploidy. If allopolyploidy is not over-represented among apomicts, it suggests that either polyploidy predated apomixis or apomixis predated the complete exclusion of pollen (see above).

Phylogenetic Patterns in the Origin and Spread of Apomixis

It is difficult to determine the rate of appearance of apomictic lineages via mutation because apomixis can also spread via hybridization. Apomixis often appears repeatedly in closely related species assemblages known as agamic complexes (Grant 1981). This pattern could indicate that apomixis arises more

readily in some groups or that it spreads more easily in these groups. Our work in two North American agamic complexes in the Asteraceae is used here to illustrate the challenges in interpreting the origins and spread of apomixis in systems with complex phylogenetic histories.

The North American *Crepis* agamic complex includes seven taxonomic species and more than 100 apomictic forms. This group was studied extensively in the 1920s and 1930s by Babcock and Stebbins, who conducted morphological and cytological surveys to characterize patterns of variation. Seven of the species include both sexual diploids and polyploids that can be sexual but are more often apomictic. Although most polyploid apomicts are assigned to one of these seven taxonomic species along with diploid sexuals, polyploids often combine characteristics of two or more diploids. The remaining two species, *Crepis barbiger*a and *Crepis intermedia*, are termed “agamospecies,” known only as polyploid apomicts with distinct morphological characteristics. All taxonomic species in the complex are connected through an intricate web of hybrid apomictic polyploids, and no part of the complex is completely genetically isolated from the rest (Babcock and Stebbins 1938; Whitton 1994). We are using phylogenetic analyses of populations within the agamic complex to infer evolutionary relationships among members of the complex, to clarify taxonomic treatments, and to shed light on the origins and spread of apomixis. Here, we describe results of a study examining phyloge-

netic affinities of the agamospecies *C. barbiger*a using variation in chloroplast DNA.

*Crepis barbiger*a is most common in the dry regions of central and eastern Washington and occurs less frequently in adjacent Idaho and Oregon. Across its range, it overlaps with a number of other species in the agamic complex. The most common taxa occurring within the range of *C. barbiger*a are *Crepis acuminata*, *Crepis atribarba*, and *Crepis modocensis* ssp. *rostrata*. Babcock and Stebbins hypothesized that *C. barbiger*a is a complex derivative of these three taxa. Because *C. intermedia*, *Crepis occidentalis*, and *C. modocensis* ssp. *modocensis* are also sympatric with these taxa and overlap morphologically, we also included these species in our study.

Three strongly supported nodes emerge from our analysis (fig. 1). We find that populations identified as *C. barbiger*a (following the keys of Babcock and Stebbins 1938) occur in at least two distinct clusters, one northern (Washington) and one southern (Oregon), with populations of the other taxa, including *C. atribarba* and *C. intermedia*, intermingled within these two clades. Populations of *C. modocensis* ssp. *modocensis* and *C. occidentalis* occupy a somewhat distinct position on these trees. Although there is taxonomic uncertainty about whether northern and southern populations of *C. barbiger*a should be treated as conspecific (*C. Sears*, personal communication), the general lack of correspondence between the chloroplast phylogeny and the morphological species identity suggest that

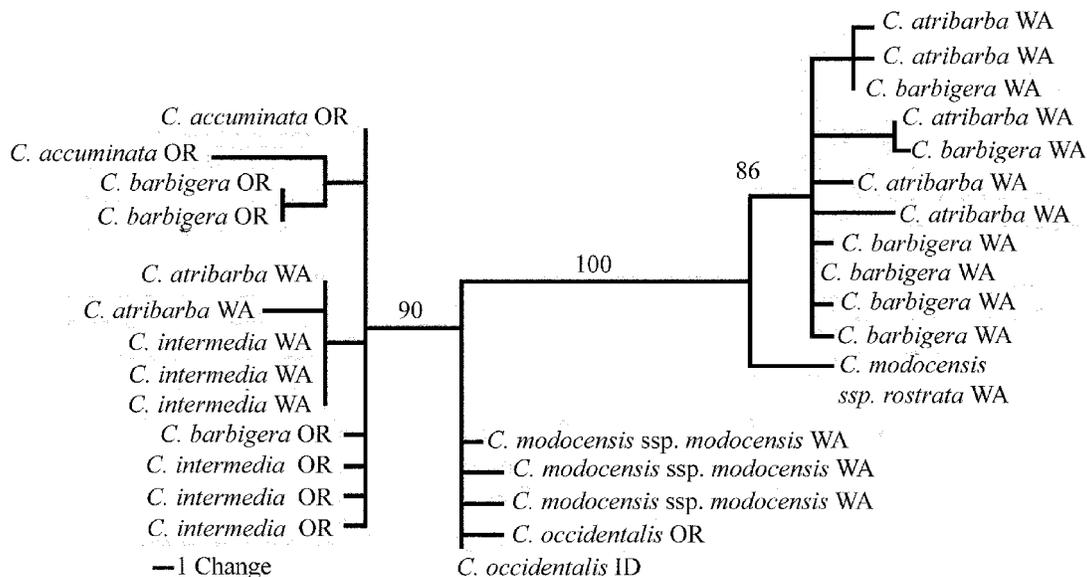


Fig. 1 Unrooted strict consensus of tree from 120 maximum parsimony analysis of four cpDNA regions for samples of the North American *Crepis* complex from Washington and Oregon. Bootstrap support values of more than 50% are indicated above the nodes. Sampled individuals represent seven populations of *Crepis barbiger*a, two populations of *Crepis acuminata*, four populations of *Crepis atribarba*, two populations of *Crepis modocensis*, four populations of *Crepis intermedia*, and two populations of *Crepis occidentalis*. Genomic DNA was isolated from field-collected leaf samples dried in silica gel using a modified CTAB protocol (Michiels et al. 2003). Four chloroplast DNA regions (*trnG*, *Rpl16*, *rps16*, and *trnM-trns*; Shaw et al. 2005), covering ca. 3507 bp, were sequenced in both directions using Big Dye chemistry and were run on an Applied Biosystems 3730S 48-capillary sequencer at the University of British Columbia Nucleic Acid Protein Service unit. Raw sequences were proofread and edited in Sequencher, version 4.2.2, and were manually aligned in Se-Al, version 2.0a (Rambaut 1996). Nucleotide substitutions and unambiguous indels were used as characters in phylogenetic analysis. Thirty-five phylogenetically informative characters were present in the combined data set. The data were analyzed using PAUP, version 4.0b (Swofford 2003), under the maximum parsimony criterion with heuristic search, using 1000 replicates and tree-bisection-branch swapping on the best trees only.

polyploid apomicts in *Crepis* have a complex history of hybridization, in agreement with previous studies (Babcock and Stebbins 1938; Holsinger et al. 1999). The existence of gene flow within the complex suggests that apomixis might have spread via hybridization. It is also possible that diploid hybrids have increased frequencies of unreduced gamete formation and that this contributes to both increases in ploidy level and enhanced expression of apomixis. Although seemingly less parsimonious, it is also possible that apomixis has arisen de novo multiple times. Our understanding will be greatly enhanced if we can follow the evolutionary history of genes underlying apomixis. In such an interconnected reticulating complex, we would predict that apomixis alleles have spread extensively.

In contrast to the situation in *Crepis*, apomixis in *Townsendia* occurs in the absence of evidence of extensive hybridization, but recent work suggests that apomixis can also become repeatedly established in this group. In *Townsendia*, apomixis occurs in approximately half of the ca. 30 taxa, where it is restricted to tetraploids. All polyploids are described as autopolyploids using morphological criteria (Beaman 1957). Autopolyploid origins of apomicts are indicated in *Townsendia hookeri* (Thompson and Whitton 2006) because there is no evidence of morphological hybridity in diploid or polyploid populations. All sampled *T. hookeri* polyploids have chloroplast haplotypes that either are identical to or recently derived from those of diploid conspecifics. Phylogenetic analysis of *T. hookeri* chloroplast DNA suggests a minimum of four evolutionary transitions from sexual diploidy to apomictic polyploidy (Thompson and Whitton 2006), but it seems more plausible that the alleles for apomixis spread into these four lineages rather than invoking four distinct origins of apomixis alleles. Alternatively, apomixis alleles may represent a shared ancestral polymorphism that gains expression in polyploid populations of *T. hookeri* (and possibly other apomictic townsendias). It is difficult to explain how apomixis alleles could persist in diploids, unless the expression of apomixis is somehow ploidy dependent. Once again, we find that a clear understanding of trait evolution will be greatly advanced by the ability to track the history of apomixis alleles.

Pathways for the Spread of Apomixis

Given that an apomict arises within a sexual population, there are two primary ways for asexuality to spread over space: direct dispersal via apomictic seed and indirect transmission via pollen. In addition, apomixis genes can spread via any sexual seeds produced by an apomictic parent and through vegetative propagation. Vegetative spread tends to be geographically circumscribed and is less likely to differ between apomicts and related sexuals (but see O'Connell and Eckert 1999).

Direct Dispersal

The direct dispersal of apomictic progeny is the most obvious and straightforward means by which the trait could spread over space. Indeed, it is commonly assumed that asexual plants should spread at an even higher rate than sexual relatives because they avoid the costs of sex (Maynard Smith 1978). However, this assumption may not be valid as surveys conducted in a number of apomicts (e.g., *Antennaria* [Bayer

1989] and *Townsendia* [Thompson et al. 2008]) find that single clones tend to be geographically restricted to one or a small number of populations (summarized originally in Ellstrand and Roose 1987). Further studies are needed to confirm these findings, which suggest that apomictic lineages rarely become widespread through seed dispersal alone.

That asexuals do not appear to have a major advantage through proliferation suggests the need to reexamine assumptions regarding the costs of sex. If an asexual mutant makes no investment in male function and is able to reallocate these resources to seed production, then the asexual lineage is predicted to have a direct twofold transmission advantage. This assumes that competing sexual species allocate reproductive resources equally to male and female functions, as is predicted to occur among outcrossing species. One factor that could reduce the cost of sex paid by related sexuals is selfing, as allocation to male function is predicted and observed to be lower among selfers (Ritland and Ritland 1989; Parachnowitsch and Elle 2004). However, apomixis tends to arise from self-incompatible progenitors (Asker and Jerling 1992; see Roy 1995 for a notable exception in *Boechea* [formerly *Arabis*] *holboellii*), which are likely to suffer from the full cost of sex. Of course, apomicts will gain benefits from avoiding the cost of sex only if the reallocation to female function accompanies the appearance of apomixis (Maynard Smith 1978; Mogie 1992). Because mutations that produce meiotic abnormalities in ovules often do not affect pollen development, the transition to apomixis need not reduce pollen investment. This suggests that the initial spread of apomixis may be little aided by reallocating resources away from male function. Empirical studies examining the immediate consequences for male fertility are needed in novel apomicts to quantify the extent to which they pay less of a cost of sex.

Over the longer term, as investment in pollen declines, apomictic lineages should begin to reap the full benefits of avoiding the costs of sex. Two studies demonstrate that established apomicts may gain a nearly twofold reproductive advantage. Meirmans et al. (2006) compared allocation patterns of naturally occurring male sterile and male fertile apomictic dandelions. They found significantly greater (but not twofold) reallocation in the form of fruit number in male sterile plants. O'Connell and Eckert (2001) provide evidence of a twofold advantage in apomictic females of the dioecious *Antennaria parlinii*. We thus expect a transition to occur as pollen investment declines, with young apomictic lineages having little fertility advantage over related sexual populations, whereas older apomicts gain from a reduced cost of sex.

Indirect Transmission via Pollen

The previous discussion assumes that pollen production only slows the spread of apomixis, but this need not be true. Ironically, the genes for maternal clonality can be transmitted via male gametes, and this mode of transmission may well be important in the establishment and spread of apomixis. That the genes for apomixis can be transferred to sexuals via the pollen of apomicts has long been known. Experimental crosses have made use of the pollen of apomicts beginning in the 1940s (Asker and Jerling 1992; e.g., Tas and Van Dijk 1999; Brock 2004), and this has become the prevalent means of

studying the inheritance of apomixis (Noyes and Rieseberg 2000).

Although individual crossing studies provide proof of principle for the inheritance of apomixis via the pollen of apomicts, studies of wild-collected individuals are just beginning to uncover the importance of this mechanism in nature. Surveys of apomictic populations have documented patterns of isozyme and cpDNA variation consistent with multiple origins of apomixis or transmission of apomixis via pollen (Roy and Rieseberg 1989; Sharbel and Mitchell-Olds 2001; Thompson and Whitton 2006). However, so far these data do not allow assessment of the frequency of transmission of apomixis via pollen.

The transmission of apomixis genes to sexuals via pollen may be of long-term importance for the spread of apomixis, even if these events are relatively infrequent. Thus, although it is straightforward to examine the reproductive mode of open-pollinated seed of sexuals for evidence of transmission of apomixis, tools that facilitate screening of large numbers of progeny may be necessary to allow detection of rare events and document this pathway in nature. Two recently developed approaches could prove essential in understanding the role of pollen in the transmission of apomixis. Flow cytometric seed screening (FCSS; Matzk et al. 2000) can be used to assess the relative ploidy of endosperm and embryo and thus to determine the genetic origin of seeds. For example, a tetraploid autonomous apomict is expected to have a 4 : 8 embryo : endosperm ploidy ratio (assuming that two unreduced polar nuclei fuse to form the endosperm), while a sexual tetraploid would have a 4 : 6 ratio (assuming that two reduced polar nuclei fuse with a reduced pollen nucleus). To date, the use of this approach has focused mainly on estimating the rate of sexual and asexual reproduction in apomicts (Matzk et al. 2000), but these data can also indicate that pollen from apomicts sires seed (Talent and Dickinson 2007). FCSS can be applied to natural or to experimental populations of mixed sexuals and asexuals. Mártonfiová (2006) applied FCSS to experimentally produced progenies, involving crosses with sexual diploids and apomictic triploids and tetraploids in *Taraxacum* sect. *Ruderalia*. If triploids were used as pollen parents, all 11 diploid mothers examined produced some triploid progeny. However, none of the 35 open-pollinated diploid mothers produced triploid seed. This suggests that detection of gene flow between sexual diploids and apomictic polyploids in nature may require intensive sampling. One unfortunate limitation of this approach is that seeds are sampled destructively, precluding later evaluation of the reproductive mode of the offspring. In an alternative approach, Bicknell et al. (2003) made use of transgenic *Hieracium pilosella* individuals carrying antibiotic resistance to track the reproductive dynamics of two facultatively apomictic individuals. Although this approach is limited to systems in which transformation protocols have been worked out, it allows screening of large numbers of seeds and efficient recovery of rare sexual offspring under experimental conditions.

To the extent that pollen from apomicts fertilizes ovules in sexual individuals and produces apomictic offspring, apomictic lineages will gain a transmission advantage even if they do not reallocate resources from male to female function (Maynard Smith 1978; Holsinger 2000; Britton and Mogie 2001). Apomicts are 100% related to the seeds that they produce directly

(compared with 50% in obligate outcrossers) as well as being 50% related to the seeds that they sire via pollen. If pollen success is similar among apomicts and sexuals, this would generate a 3 : 2 transmission advantage that parallels the transmission advantage enjoyed by selfers arising within outcrossing populations (Maynard Smith 1978; Uyenoyama 1984; Holsinger 2000). The magnitude of the transmission advantage will depend on levels of pollen viability in new apomicts, about which little is known. In established apomictic populations of *T. hookeri*, pollen viability averaged 17%, with the highest viability being 42% (Thompson and Whitton 2006). However, Noyes et al. (2007) produced a novel apomict with 98% viable pollen.

Maynard Smith (1978, p. 41) noted that as the frequency of apomixis rises, transmission via pollen becomes less efficient, and thus, one would expect pollen fertility to decline (through drift or selection; Maynard Smith 1978; Eckert 2002). Because apomixis would not enjoy a transmission advantage within a highly selfing population (in which outcross pollen is rarely incorporated), the observation that apomixis typically arises from self-incompatible species (Asker and Jerling 1992) suggests that the initial transmission advantage arising from producing pollen as well as apomictic seeds might be important to the spread of apomixis. Interestingly, apomicts also tend to maintain pollinator attraction features and are not associated with reduced flower size, again suggesting that pollen transmission continues to be important in these taxa.

When pollen from apomicts fertilizes sexual ovules, this allows the genes for apomixis to move into multiple genetic backgrounds; this is perhaps even more important than the transmission advantage gained. As pointed out by Mogie (1992), this movement might be key to the evolutionary success of apomicts. Gene flow via pollen improves the chance that apomixis will be associated with a genotype of high fitness, increasing the probability of successful establishment. The spread of apomixis via pollen also increases the genetic variability of asexual populations, improving their ability to respond to selection and to adapt to new habitats. Indeed, patterns and levels of diversity within and among apomictic populations reveal substantial variation (Ellstrand and Roose 1987; Silvertown 2008). Thus, the occasional capture of different sexual genetic backgrounds via pollen flow from apomicts may provide many of the evolutionary benefits of sex and recombination to predominantly asexual plant populations (further discussed in "Apomixis and the Evolution of Sex").

Apomixis genes may also be transmitted via sexually fertilized seeds produced by otherwise apomictic plants (Asker and Jerling 1992; Matzk et al. 2000; Bicknell et al. 2003; Richards 2003). If this process involves meiotically reduced eggs, the apomict would lose its transmission advantage with respect to these seeds (which bear only half of the genes of the maternal apomictic parent). If unreduced eggs were involved, the apomict would continue to transmit the same number of genes to the next generation via these seeds, but the seeds would have an increased ploidy level and might well be less fit. Thus, we would expect a lower transmission advantage in apomicts that often act as maternal parents of sexually produced seed. However, to the extent that this pathway allows apomixis to be expressed in novel genetic backgrounds, it too may increase the likelihood of persistence.

Geographical Parthenogenesis

That sexual and asexual relatives tend to have nonoverlapping ranges in both plants and animals has long been noted, resulting in a pattern termed “geographical parthenogenesis” by Vandel (1928). The distributions of a number of taxa reveal that asexuals are likely to occupy latitudes and elevations higher than those occupied by their sexual counterparts. Data relating to geographical parthenogenesis in plants are summarized by Bierzychudek (1985) and Hörandl (2006).

Explanations for the existence of geographical parthenogenesis generally fall into either ecological or demographic categories. Ecological explanations are based on differential ecological tolerances or competitive abilities of sexuals and asexuals. For example, it has been proposed that asexuals may comprise general-purpose genotypes (Lynch 1984) that can occupy a wide range of ecological conditions but are relatively poor at tracking extreme or specialized habitats. Support for the existence of general-purpose genotypes in plants is, however, sparse. Although it might seem unlikely that multiple genetically distinct lineages of apomicts would have hit on similar general-purpose genotypes, independent lineages of apomicts might exhibit similar ecological features as a result of parallel polyploidization events; polyploidy often induces specific morphological changes, altered ecological tolerances, and shifts in gene expression (Otto and Whitton 2000; Adams and Wendel 2005). We are aware of no studies to date that examine the ecological response of multiple lineages of a single apomict.

Demographic explanations attribute the distribution of sexuals and asexuals to the relative dispersal and establishment abilities of apomicts. In addition to the ability to found populations with a single propagule, apomicts may be favored during recolonization of previously glaciated habitats because of the scarcity of potential pollen sources and pollinators. We would thus predict that apomicts that colonize deglaciated areas would more often be autonomous or be able to use self pollen to initiate endosperm. Once established in these habitats, apomictic plants could exclude sexual relatives, owing to frequency-dependent fitness effects described below.

Because in plants geographical parthenogenesis tends to involve gametophytic apomixis and because such apomicts tend to be polyploid (unlike with adventitious embryony), Bierzychudek (1985) suggested that polyploidy rather than asexuality may be the key contributor to the distributional patterns. Stebbins (1950) also observed that sexual polyploids tend to have more northerly and higher-elevation distributions than related diploid sexuals. Brochmann et al. (2004) confirmed that polyploids are more prevalent in the arctic but noted that this trend applied mainly to higher ploidy levels (greater than tetraploid) and to floras in previously glaciated regions. More frequently, authors suggest that asexuality rather than polyploidy is key in establishing the pattern (Hörandl 2006; Thompson and Whitton 2006). The relative contributions of apomixis and polyploidy to geographic patterns will be best explored in systems in which both sexual and apomictic polyploids are known, such as in the *Antennaria parlinii* complex (Bayer and Stebbins 1983).

Polyploidy and apomixis may also interact in a manner that contributes to geographical parthenogenesis, through a phenomenon known as destabilizing hybridization (Lynch 1984). Interploidy crosses in sexually reproducing groups can generate

strong reproductive incompatibilities through the formation of inviable or sterile offspring (e.g., triploid block; Ramsey and Schemske 1998; Burton and Husband 2000). Where sexual diploids and asexual polyploids co-occur, hybridization asymmetrically reduces the fitness of sexual diploids because sexuals are more likely than apomicts to incorporate pollen from other ploidy levels, leading to offspring of odd ploidy levels. Thus, all else being equal, the presence of asexuals can destabilize sexual populations. Sexuals might therefore persist only in portions of the range where they have a selective advantage over asexuals. In this regard, it is noteworthy that in both *Crepis* and *Townsendia*, diploids tend to occupy habitats that could be described as more specialized. For example, in *T. hookeri*, diploids occur on Niobrara and Pierre shales, with soils that are significantly higher in selenium, aluminum, and other elements known to restrict the distribution of plants in other groups (E. M. Stacey and J. Whitton, unpublished data). The restriction of diploids to these unusual substrates may indicate that they hold a selective advantage under these conditions.

Apomixis and the Evolution of Sex

One of the longest-standing questions in evolutionary biology is why sex is so prevalent. That apomixis arises repeatedly in plants but fails to take substantial hold suggests that plants may shed light on the benefits of sex and the costs of asexuality. Here, we discuss how the emerging data on apomixis informs the literature on the evolution of sex and vice versa.

To structure this discussion, we focus on three interrelated questions: Why are there no ancient asexual angiosperms? Why do few plant populations exhibit mixtures of sexual and asexual individuals? And why don't most plants reproduce apomictically while engaging in occasional sex?

Why Are There No Ancient Asexual Angiosperms?

Although apomixis may appear fixed or nearly so within particular populations or portions of a species range, the only known instance of a phylogenetically isolated apomictic lineage in seed plants is *Houttuynia*, a small (perhaps monotypic) genus in Saururaceae, first reported as apomictic by Okabe (1930). However, it is not clear that the entire lineage is apomictic. Even if it is, whether the loss of sex occurred early or late in its evolutionary history is not known. All remaining angiosperm apomicts are at the tips of the tree of life, with no other higher-level taxa (families, genera) that are asexual. A number of well-studied temperate apomicts have geographic distributions consistent with an origin following Pleistocene glaciation, suggesting that these apomicts may be of very recent origin (Hörandl 2006; Thompson and Whitton 2006). Despite this phylogenetic distribution, there are indications that the tendency to produce apomictic lineages may have arisen early in the diversification of some deeper lineages. For example, apomixis in the Rosaceae occurs within species of numerous genera. Recent phylogenetic results (Potter et al. 2007) reveal that *Rubus*, which contains a number of apomicts, diverged early in the evolutionary history of subfamily Rosoideae. This suggests that the tendency to generate apomicts may have appeared early within this lineage. Although a predisposition

toward apomixis might persist for long periods of evolutionary time, apomictic lineages, once produced, have only a shallow phylogenetic history in seed plants, with no truly ancient asexual taxa.

Why apomictic lineages of angiosperms appear to be restricted to the very tips of evolutionary branches remains unclear. Ancient asexual lineages appear in other groups, most notably bdelloid rotifers and darwinulid ostracods but also among ferns, where vegetatively reproducing *Vittaria* sp. and *Trichomanes* sp. are estimated to be ca. 10 million years old (Farrar 1990).

Recent theoretical work on the evolution of sex has highlighted the importance of maintaining sex and recombination in populations that are limited in size because genetic variation can be rapidly depleted by the combined action of drift and selection (see reviews in Otto and Gerstein 2006; de Visser and Elena 2007). Genetic variation in fitness is particularly limited in asexuals because of their inability to bring together high-fitness alleles that reside in different individuals. Consequently, any advantage that apomicts might initially have is thought to decrease over time because of (a) the accumulation of deleterious mutations (Muller 1932; Keightley and Otto 2006), (b) a reduction in the rate of adaptation due to beneficial mutations that arise in different individuals and cannot be brought together in apomicts (the Fisher-Muller hypothesis; Morgan 1913; Fisher 1930; Muller 1932; Barton and Otto 2005), and (c) a greater loss of beneficial mutations because they happen to arise in genomes carrying deleterious mutations (the ruby-in-the-rubbish hypothesis; Fisher 1930; Peck 1994). In each case, the fortune of apomicts is predicted to decline over evolutionary timescales because of the difficulty of combining fit alleles.

In this context, there are two potential ways for obligate asexual species to avoid extinction. First, an asexual lineage could avoid the accumulation of deleterious mutations if mutation rates happen to be particularly low. Such a lineage would be unable to adapt rapidly, but if its environment were sufficiently stable, it might avoid extinction. Some data suggest that darwinulid ostracods might have hit on this long-term solution because ostracods have unusually low mutation rates (Butlin and Menozzi 2000; Schön et al. 2003). Second, if an asexual species has a sufficiently large population size and a high migration rate among populations, genetic variation within local populations could remain high enough to allow asexuals to evolve at a rate akin to that of sexual competitors (Ladle et al. 1993; Judson 1995; Martin et al. 2006; Salathé et al. 2006). This is perhaps the route taken by bdelloid rotifers because analyses of sequence data suggest that dispersal rates are high, genetic diversity levels are similar to those of sexual populations, and the ability to respond to selection is similar to that of sexual monogonont rotifers (Birky et al. 2005).

So why aren't there ancient asexual plants? Perhaps the special circumstances enabling asexuals to persist over long periods of evolutionary time do not co-occur in plants. Estimates obtained to date of the genome-wide deleterious mutation rate are high in angiosperms (typically above 0.1 per generation; Drake et al. 1998; Schoen 2005). Furthermore, as a result of limited seed dispersal and low rates of gene flow via pollen, strong spatial structure with isolation by distance is likely to exist in many apomictic species (Meirmans et al. 2003), suggesting that genetic variation within local popula-

tions is not replenished at high rates by migration (Thompson and Whitton 2006; Thompson et al. 2008).

Why Do Few Plant Populations Exhibit Mixtures of Sexual and Asexual Individuals?

Characterization of reproductive mode in apomictic complexes suggests that it is uncommon for local populations to be composed of substantial numbers of both primarily sexual and primarily apomictic individuals (Beaman 1957; Gadella 1987; Asker and Jerling 1992; O'Connell and Eckert 1999). Where co-occurrence has been documented, it often results from secondary contact between sexuals and apomicts, producing complex sexual-asexual dynamics (Verduijn et al. 2004; Noyes and Allison 2005; Thompson et al. 2008; K. M. Dlugosch, C. J. Sears, and J. Whitton, unpublished manuscript). A notable exception occurs in *Taraxacum*, in which ploidy cycles, with accompanying switches between sexuality and apomixis, seem to arise on shorter timescales (Meirmans et al. 2003; Verduijn et al. 2004), based on studies of standing variation.

That populations tend to be predominantly apomictic or predominantly sexual is consistent with models exploring the outcome of competition between asexuals and sexuals. In a number of ecological models, it is assumed that whatever advantage(s) sex has in the long run can be modeled as a fixed fitness advantage (Joshi and Moody 1995, 1998; Bengtsson and Ceplitis 2000; Britton and Mogie 2001; Carrillo et al. 2002). Under these assumptions, whether apomicts spread to fixation depends on the assumed fitness advantage of sexuals, the relative pollen output of the apomict, the ability of apomicts to reallocate male function, and the relative success of male gametes from apomicts (Joshi and Moody 1995). In both spatial (Britton and Mogie 2001; Carrillo et al. 2002) and non-spatial (Joshi and Moody 1995; Bengtsson and Ceplitis 2000) versions of these models, it is difficult to maintain sexuals and asexuals together indefinitely. Thus, these models predict that either sexuals or asexuals will win out within a population, depending on the exact balance of selective forces.

These models assume that the benefits of sex are fixed, which is unlikely to be true. For example, newly formed apomicts may suffer little or no loss of viability compared with sexuals because there has been little time for mutation accumulation. In contrast to these ecological models, evolutionary models track the dynamics of selected loci in sexual and asexual populations and allow the benefits of sex to emerge from differences in the response to selection. Nevertheless, evolutionary models also typically observe that either sexuality or asexuality comes to dominate a population. For example, spatially explicit models of individuals subject to recurrent deleterious mutation find that asexuals beat out sexuals when dispersal rates are high or mutation is low, while the reverse is true when dispersal is local and mutation is common (Peck 1994; Salathé et al. 2006). Similarly, in classical host-parasite models, Hamilton (1980; Hamilton et al. 1990) found that sexuals took over the population under some conditions (many parasites per host; strong selection) but that asexuals otherwise dominated.

Although local populations tend to be apomictic or sexual, both sexual and apomictic populations typically coexist on a regional or specieswide scale. This observation is consistent with

the previously discussed models if the conditions favoring sex over apomixis vary over space. Furthermore, even if one reproductive mode ultimately outcompetes the other, this process may take a long time. For example, adjacent clumps of sexuals and asexuals coexisted for thousands of years in the simulations of Britton and Mogie (2001), especially when apomictic pollen viability is low and therefore apomicts only gradually invade sexual populations from the edges.

More theoretical work is needed, however, because these models fail to capture all of the key natural history features of plant apomixis. For example, models comparing the evolutionary dynamics of mutation accumulation in sexuals versus asexuals have yet to consider the occasional transmission of apomixis via pollen. The recurrent capture of sexual genotypes via pollen might allow a stable coexistence between sexual and asexual populations, which is seen when asexuality arises by recurrent mutation (Salathé et al. 2006). Further models are also needed that explore the sorts of complex spatial patterns of selection experienced by many species with apomixis. For example, strong selection in harsh sites might favor particular genotypes, and apomicts, by avoiding recombination, might do well under these conditions. Yet, in other sites, the ability of sexual populations to respond more rapidly to selection might allow sexuals to outcompete asexuals (e.g., because of the advantages of bringing together fit alleles carried by different individuals). Thus, although most previous theory suggests that sexual and asexual individuals should not coexist over the long term, it may well be that more realistic models incorporating features commonly encountered in plant apomicts might lead to models that are more favorable to coexistence.

Why Don't Most Plants Reproduce Apomictically While Engaging in Occasional Sex?

Apomixis is typically associated with the abandonment or great diminution of recombination, but the handful of studies aimed at detecting and quantifying recombination in apomicts have found evidence for at least occasional sex in apomicts (van der Hulst et al. 2000, 2003; Chapman et al. 2004; Thompson et al. 2008). In models that allow variable levels of sex, it is commonly observed that a little bit of sex goes a long way, so it would seem that the advantages of sex and recombination could be achieved in predominantly asexual lineages that undergo occasional recombination (Green and Noakes 1995; Hurst and Peck 1996; Peck and Waxman 2000). If this were true, then why aren't all species predominantly apomicts with a small degree of sexual recombination?

Theoretical analyses have identified some conditions under which high levels of sex are favored over lower levels. For example, when hosts and parasites coevolve and are subject to strong selection, lineages with low levels of sex are invaded by lineages with high levels of sex (Peters and Lively 2007). When selection varies over space, migration can generate combinations of alleles (linkage disequilibria) that are not locally favored, which can select for high levels of sex and recombination (Lenormand and Otto 2000). When heterozygote advantage and inbreeding are present, variants with higher rates of sex can be favored over those with lower rates of sex (Peck and Waxman 2000; Dolgin and Otto 2003). Finally, even just recurrent selection against deleterious mutations can select for

high levels of sex and recombination because a little recombination is not sufficient to release genetic variation hidden by linkage disequilibrium among loci in finite populations (Keightley and Otto 2006). Thus, there are a reasonable number of models that can explain why high levels of sex have evolved and been maintained in most plants, even though reproductive systems exist that would allow apomixis with low levels of sex.

As theoretical studies accumulate that can explain the evolutionary maintenance of high levels of sex, the question turns on its head, and we must ask what special circumstances allow apomixis to gain a foothold. The pattern of geographical parthenogenesis suggests that the most common of these special circumstances might occur when populations extend into harsh environments where certain combinations of alleles must be kept together. Apomixis would then allow the possibility of a "frozen genotype" that can survive and spread beyond the geographical limits faced by sexual populations, which are subject to ongoing gene flow that disrupts the necessary genotype(s) (Peck et al. 1998). Empirical studies demonstrating that sexuals fail to adapt at the edge of their species range because of gene flow from the core of the population would provide support for this hypothesis.

Conclusions

The emerging view of apomixis in flowering plants reveals this mode of reproduction to be highly dynamic. Apomictic populations harbor substantial genetic variation, and in a growing number of cases, including *Crepis* and *Townsendia*, evidence indicates that multiple genetic lineages have been captured from related sexual populations, either through fertilization by pollen from apomicts or through multiple origins of apomixis. This dynamic nature of apomixis might be critical to its establishment and spread. In particular, gene flow via pollen produced by apomicts has the potential to affect both the spread of the trait and the ability of apomicts to appear within novel genetic backgrounds. Still, our understanding of the role of pollen in natural apomicts is limited. Future empirical studies focusing on regions of co-occurrence of apomicts and sexuals, as well as studies of apomicts that are known to reproduce sexually at moderate frequencies, will provide important insights into the role of male fertility in sexual-aseexual dynamics. Further studies are also needed to examine the properties of recently derived apomicts. For example, do new apomicts reallocate resources from male to female function and so pay less of a cost of sex? Do new apomicts have different ecological tolerances? And is this process idiosyncratic, depending on the exact genotype involved, or are there some features that apomicts have in common and that differentiate them from sexual relatives? Such studies will help to clarify the relative importance of demographic effects, ecological differences, and their interactions in the establishment and spread of apomixis, providing a broader and more complete understanding of the conditions favoring evolutionary transitions to asexuality in plants.

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