

New perspectives into the evolution of polyploid complexes

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Abstract

Polyploidy is a major evolutionary process in flowering plants that has attracted much research time and effort. New molecular evidence about the evolution of polyploids forces a re-evaluation of many old ideas about polyploidy. In addition to molecular approaches, ecological studies will make a substantial contribution to our knowledge of the evolution of polyploidy. Studying the response of polyploids and agamosperms to their environment will help us learn more about the adaptive significance of polyploidy and the strongly associated phenomenon of apomixis. New developments in the investigation of polyploid complexes that will be reviewed in this paper include (1) genome evolution during the initial stages of formation of polyploids, (2) the dynamic nature of agamic complexes with facultative apomixis, and (3) the adaptive significance of polyploidy from an ecological perspective on both a micro-habitat and macro-geographic scale. One of the most important recent findings about the evolution of polyploidy is that significant chromosomal repatterning occurs within a few generations after amphidiploid formation. Furthermore, habitat preference differs for diploids and tetraploids, although the difference in niche preference by different polyploid levels is less clear. There may be a direct correlation between wide ecological amplitude and high amounts of genetic diversity in the polyploids. Balanced polymorphism for cytotypes, as in some autopolyploids, may be adaptive because it can extend the ecological amplitude of the species. The adaptive significance of polyploidy, with respect to both sexual and agamic complexes, is that it may allow polyploids to occupy niche space not occupied by their diploid progenitors, whether they are in intermediate habitats or divergent habitats to the diploids. These are all interesting findings that have come from recent molecular and ecological studies, which indicate that polyploid complexes are very dynamic, often rapidly evolving, systems.

Keywords: polyploidy, agamic complexes, apomixis, adaptation.

Introduction

Polyploidy is a major evolutionary process in flowering plants and therefore much research time and effort has been directed toward elucidating all aspects of this phenomenon. A large amount of knowledge, such as geographic and taxonomic distribution, origins, genetic consequences, and association with apomixis, has been gained about polyploidy during this century. However, much is still to be learned, especially concerning polyploidy as a speciation mechanism, ancient vs. recent polyploids, diploidisation of ancient polyploids, factors contributing to the development of polyploid complexes (*i.e.*, what causes polyploidy to develop in certain taxonomic groups and/or floras), multiple vs. unique origins of polyploids, and the adaptive significance of allopolyploidy and autopolyploidy. It is likely that with the advent of new molecular methods, we will rapidly begin to gain new insights into some of these areas (Soltis & Soltis, 1993). This review will provide information that is applicable and informative with respect to both sexual and agamic polyploid complexes.

Evolution of polyploid sexual and agamic complexes: Sexual polyploid complexes are by far more common than polyploid agamic complexes (Babcock & Stebbins, 1938; Grant, 1981). Sexual polyploid complexes consist of at least two morphologically distinct diploids that give rise to a series of auto- and allotetraploids that span the range of morphological features of the diploid parents. The morphological distinctness of the diploids is obscured by the presence of the autopolyploids, and the entire complex forms a morphological continuum. Additional even-polyploid levels, such as hexaploids and octoploids, develop in mature polyploid complexes, and these tend to be reproductively isolated from other ploidy levels. Because members of these ploidy levels are amphimictic, individuals of divergent genetic makeup can cross with ease, forming large morphological continua within each ploidy level.

In contrast to sexual polyploid complexes, agamic complexes typically include a series of polyploid sexual, facultatively or obligately agamospermous microspecies, which are largely the result of various hybridisations among sexual diploid and sexual polyploid members of the complex. If several diploids have contributed genes to the complex, then an enormous number of microspecies evolve because each microspecies can be of different multiple hybrid origin. The sexual diploid relatives are distinct morphologically from one another, but have a much greater amount of morphological variation than any single microspecies. This is in direct contrast to the sexual polyploid complex in which each homoploid level has much more variation than the sexual diploids. Initial steps in the formation of both sexual and agamic complexes involve hybridisation among sexual diploids, which give rise to polyploids at many different ploidy levels. Generally, some of the polyploids at the lower levels in the agamic complex (triploids and tetraploids) reproduce sexually and consequently there is a possi-

bility for gene exchange among them. At higher ploidy levels, where agamospermy is primarily obligate, microspecies are reproductively isolated from one another. Morphological variation among various obligately agamospermous microspecies is slightly discontinuous because of their reproductive isolation. Some clones tend to merge morphologically into their sexual relatives, especially if they have a significant number of genes from a single sexual taxon. Consequently, this obscures the morphological distinctness of the sexual diploids themselves. Perhaps genes from the sexual diploids can continue to be relocated, via introgressive gene flow, into the agamic complex through sexual triploid and tetraploid members of the complex. Unbalanced cytotypes such as triploids, pentaploids, heptaploids, and various aneuploids can reproduce easily via agamospermy and therefore any hybrid has the potential to become fertile. This contrasts with the polyploid sexual complex in which odd-polyploid levels are rarely encountered. The resultant polyploid agamic complex is comprised of a myriad of clones that appear morphologically to represent a giant hybrid swarm, which is usually of multiple hybrid origin from among several sexual relatives and can contain everything from fully sexual individuals, to facultative apomicts, to obligate apomicts (Bayer *et al.*, 1990; Bayer, 1997).

Current topics in polyploid research

The majority of the past research on polyploidy has been conducted on sexual polyploid instead of apomictic polyploid complexes. However, many of the conclusions formulated from these studies are also applicable to the agamic complex. This is especially true of young agamic complexes, which can contain complex mixtures of sexuals, facultative apomicts, and obligate apomicts (Bayer *et al.*, 1990). Much is now known about the taxonomic and macrogeographic distribution of polyploids, the types of polyploids, and the phylogenetic origin of certain polyploids. We now know that many polyploid complexes are of multiple hybrid origin (see review in Soltis & Soltis, 1993), but our knowledge is lacking with respect to what occurs during the initial stages in polyploid evolution subsequent to their formation. Do they remain largely unaltered following their origin or do they subsequently evolve rapidly? Do polyploids of different ploidy levels have different adaptive advantages in different local environments? Many unanswered questions centre on the adaptive significance of auto- and allopolyploidy and their genetic constitution. So the question might be asked, what is the adaptive significance of polyploidy in both amphimictic and apomictic complexes? Are populations in agamic complexes composed exclusively of obligate apomicts, or are they dynamic mixtures of amphimicts, facultative apomicts, and obligate apomicts? In an effort to address some of these issues, in this review I will concentrate on (1)

genome evolution during the initial stages of formation of polyploids (2) the dynamic nature of agamic complexes with facultative apomixis, and (3) the adaptive significance of polyploidy from an ecological perspective on both a micro-habitat and macro-geographic scale.

Polyploidy - the early stages

Although we have a fairly good idea that the initial steps in the formation of most polyploids involve multiple separate hybridisations, we have little information about what happens subsequent to their formation. The most thorough work that has been done on later-generation polyploids is found in a series of papers by Song *et al.* (1988, 1993, 1995) in the U-triangle of *Brassica* species (U, 1935). The three diploid *Brassica* species in the U-triangle, *B. rapa* (A genome), *B. nigra* (B genome) and *B. oleracea* (C genome) gave rise to three amphidiploids *B. napus* (A/C), *B. juncea* (A/B), and *B. carinata* (B/C) (U, 1935; Song *et al.*, 1988). In their series of experiments, Song *et al.* (1988, 1993, 1995) hybridised the diploids in all combinations of reciprocal crosses. The F1 hybrids were then polyploidised using colchicine. Nuclear, mitochondrial and chloroplast genetic RFLP markers were identified using 89 probes (Song *et al.*, 1995). The parental diploids and all subsequent generation polyploids (up to the F3) were characterised genetically. The diploids were divergent at several loci, providing each with a large number of unique genetic markers. The diploids used in the crosses were inbred lines and thus homozygous for the genetic markers (Song *et al.*, 1995). This assured that the doubled hybrids were also homozygous, and therefore changes seen in the later-generation hybrids were real genetic changes, not the result of genetic segregation. Some of the basic findings of the study help substantiate the notion that genetic diversification in polyploids can occur over a relatively short period of time (Song *et al.*, 1995).

Interestingly, the F3 plants had the same organellar DNA fragment patterns as their F2 parents, but the nuclear DNA fragment patterns differed greatly (Song *et al.*, 1995). Substantial losses and gains of fragments were observed in some polyploid lines over the generations up to F3. Five fragment losses and 51 gains were observed in *B. nigra* x *B. rapa* amphidiploids. The relative magnitude of the genetic divergence in the nuclear genome of polyploids between the F2 and the F3 generations based on genetic distance estimates is strikingly large (ranging from 2.1 to 9.6%). A principal coordinate analysis of the RFLP data showed that the synthetic amphidiploids were almost exactly intermediate between their parents, whereas naturally occurring polyploids were more divergent, indicating that these polyploids had diverged a great deal since their origin (Song *et al.*, 1993).

However, crosses involving different diploid parents behaved differently, *B. nigra* x *B. rapa* amphidiploids evolved twice as many differences as *B. oleracea* x *B. rapa* amphidiploids (Song *et al.*, 1995). There appears to be a direct correlation between the degree of relatedness of the diploids and amounts of change in the polyploid derivatives. Parents that are known to be more distantly related (*B. nigra* and *B. rapa*) yield polyploids that have higher frequencies of genome changes than do ones that are closely related (*B. oleracea* and *B. rapa*). Evidently there is more genetic instability caused by cytoplasmic-nuclear incompatibilities in these amphidiploids that result from the wider crosses and this leads to more rapid changes in those hybrids (Song *et al.*, 1995). Directional changes, where losses of fragments unique to one parent predominated over those from the other parent, were apparent. Finally, reciprocal cross amphidiploids differ in their morphological resemblance to their parents, often resembling their maternal parent more closely and often having higher frequencies of genome change from fragments attributable to their maternal parent than their paternal (Song *et al.*, 1995).

The major outcome of this work is that it demonstrates that newly formed polyploids can undergo substantial and rapid changes following their origins and that the cytoplasm of the new polyploid can dramatically affect the genetic changes that follow. Evidently the cytoplasm can cause a harmonious balance to occur between itself and the nuclear genetic background (Song *et al.*, 1995). No one knows how this drama would play out in nature, but such studies are needed.

A similar study to that of Song *et al.* (1995) involves artificial polyploid synthesis in hexaploid wheat (*Triticum aestivum* L.) by Feldman *et al.* (1997). Artificial polyploids were created using *T. uratu* Tumanian ex Gandilyan, *Aegilops speltoides* Tausch, and *A. tauschii* Coss., representing the A, B, and D wheat genomes respectively. Feldman *et al.* (1997) used 16 low-copy, chromosome specific (CSSs) and genome specific sequences (GSSs) as probes. The synthetic polyploids were grown out to the S₅ generation. As with the *Brassica* study (Song *et al.*, 1995), Feldman *et al.* (1997) found extensive loss and gain of RFLP fragments over the generations, however they found that the elimination of sequences in the polyploids was non-random. The same sequences were always lost from the genome in all the plants; this contrasts with the findings of Song *et al.* (1995), who found a random loss and gain of fragments among their synthetic polyploids. They concluded that the elimination of sequences occurs through a precise mechanism and that this may be adaptive, as it perhaps reduces redundancy of gene expression (dosage compensation). They reiterated the findings of Song *et al.* (1995) that extensive genome modifications can occur over a relatively short time. Most recently, Liu *et al.* (1998) used synthetic hexaploid wheat and *Aegilops* L. to investigate changes in 43 coding sequences over up to six generations. They found that only three specific types of changes occurred, disappearance of a

parental hybridisation fragment(s) for some enzymes, appearance of novel fragments, or coincidental loss of parental fragment(s) and appearance of novel ones (Liu *et al.*, 1998). There was never any complete elimination of parental fragments for a given probe. This contrasts with the earlier study (Feldman *et al.*, 1997), where certain non-coding parental sequences were completely lost in some cases. The changes that were brought about may be due to methylation of the region, which inactivates the sequences or changes their expression, but doesn't eliminate them.

Often novel molecular techniques can open up robust new ways to investigate polyploid evolution (Soltis & Soltis, 1993) and the relatively new field of molecular cytogenetics is just such a technique. Molecular cytogenetics on the natural tetraploid *Nicotiana tabacum* L., documents the chromosomal repatterning that occurs widely in polyploids subsequent to their formation (Kenton *et al.*, 1993). The diploid S-genome of tobacco (*N. sylvestris* Speg. & Comes) and T-genome (either *N. otophora* Griseb. or *N. tomentosiformis* Goodsp.) were used as probes in a genomic *in situ* hybridisation experiment (GISH) to probe the chromosomes of common tobacco, *N. tabacum*. The labelled genomic DNA of *N. sylvestris* hybridised to entire chromosomes of *N. tabacum*, as well as parts of other recombinant chromosomes (Kenton *et al.*, 1993). When the labelled genomic DNAs of *N. otophora* or *N. tomentosiformis* were hybridised to the chromosomes of *N. tabacum*, only the DNA of *N. otophora* hybridised to entire chromosomes or portions of recombinant chromosomes. The DNA of *N. tomentosiformis*, which has often been selected as the most likely source of the T-genome, hybridised to scattered spots along all of the chromosomes giving them a mottled appearance. It was suggested that the probe DNA was hybridising to dispersed repeated sequences (Kenton *et al.*, 1993). The probe DNA from *N. tomentosiformis* hybridised in a similar, mottled pattern to *N. otophora* (as well as in reciprocal experiments), suggesting introgressive hybridisation between the two. Therefore, it is likely that the source of the T-genome in *N. tabacum* is *N. otophora*, or perhaps *N. otophora* introgressed with *N. tomentosiformis* (Kenton *et al.*, 1993). The most important findings of this work to the evolution of polyploidy is that it demonstrates that significant chromosomal repatterning occurs in the amphidiploids subsequent to their formation.

Facultative apomixis and the dynamic polyploid agamic complex

One cannot always classify polyploid complexes as either sexual or agamic because in some cases sexual populations and apomictic populations exist within the same polyploid complex. Indeed in some cases, sexual individuals, facultative apomicts, and obligate apomicts co-exist within the same population, *e.g.*, in dioecious *Antennaria*

media E. Greene (Bayer *et al.*, 1990). The inter-plant variation in sexual and asexual reproduction in an Oregon population of the alpine perennial, *A. media*, was investigated (Bayer *et al.*, 1990). Four polymorphic loci were assayed by enzyme electrophoresis of the progeny of 72 families from two spatially distinct subpopulations. A multilocus model, incorporating a mixture of apomixis and random outcrossing, was used to estimate the mating system of pistillate plants both on the population and individual levels with statistical significance of the estimates based on bootstrap methods (Bayer *et al.*, 1990). The population contained a mixture of sexual individuals, partial apomicts, and obligate apomicts. The first subpopulation contained individuals that were partially apomictic and presumably produced both reduced and unreduced embryo sacs. There was a conspicuous difference in the breeding system composition between the two subpopulations. The first subpopulation had a 'female' biased gender ratio and contained mostly obligate apomicts, some partial apomicts, and some outcrossing amphimicts. The second subpopulation, which had a nearly balanced gender ratio, contained mostly amphimicts, some obligate apomicts, but no facultative apomicts. This was the first study to document partial apomixis in individual plants by the use of genetic markers. Our study of these dynamic subpopulations points to the fact that the reproductive structure of populations of *Antennaria* may not be as simple as once believed. Perhaps under certain conditions partially apomictic populations like these have the advantage over fully sexual or apomictic populations in being able to change the relative proportions of sexual and asexual individuals as selection acts to change their relative advantages. Also, presence of facultative apomicts in gynoecious populations of gametophytic apomicts, such as *A. rosea* Greene, may be a result of more frequent genesis of new clones in these populations through backcrossing to sexual tetraploid relatives, such as *A. umbrinella* Rydb. (Bayer, 1990c). Clausen's "Henry Ford" or "model T" hypothesis (Clausen, 1954; Marshall & Brown, 1981) concerning the adaptive significance of apomixis may apply to the case of *A. rosea*, where facultative sexuality continually supplies the necessary genotypes to be tested, but only the most successful ones are 'reproduced authentically' and continuously via apomixis. Thus, facultative amphimicts may play a very important role in the maintenance of clonal diversity in the *A. rosea* complex. Additional studies, to elucidate the role of partial apomicts in the evolution of the agamic complex are greatly needed. Recently, Nybom (1995) has used minisatellite probe M-13 to document low levels of facultative apomixis in European blackberries (*Rubus* subgen. *Rubus*). Campbell *et al.* (1994) have used RAPD markers to explore levels of apomixis in *Amelanchier* Medic. They uncovered low levels of sexuality in predominantly apomictic clones of *Amelanchier laevis* Wieg. Both these studies (Campbell *et al.*, 1994; Nybom, 1995) disclose the possibility that relatively new genetic markers like minisatellites, RAPDs, and possibly

production was quite variable, but it was frequently significantly higher in enneaploids than in the hexaploids (Keeler & Davis, in press). Total reproductive effort was significantly greater for enneaploids than for hexaploids, as measured by mass, but germination of caryopses was significantly greater for hexaploids (Keeler & Davis, in press). On a per plant basis, however, enneaploid plants produced more viable caryopses. The predominance of both hexaploids and enneaploid individuals in mixed populations is best explained by offsetting selection, where hexaploids produce fewer flowers, but a higher percentage of viable fruits, and enneaploids producing greater biomass (more flowers; but proportionally fewer good fruits) overall produce more good caryopses (Keeler & Davis, in press). It can be concluded that balanced polymorphism for cytotypes may be adaptive because it can extend the ecological amplitude of the species (Keeler & Davis, in press). Intraspecific polyploidy, as a form of genetic variation, is worthy of future investigation.

Bayer *et al.* (1991) and Brochmann & Elven (1992) looked at the adaptive significance of polyploidy on a macro-habitat scale. Both studies looked at the spatial distribution of diploids and associated allopolyploids, the origin of which has been thoroughly documented (Brochmann *et al.*, 1992a, 1992b, 1992c; Brochmann & Elven, 1992; Bayer, 1989, 1990a, 1997). The studies took different approaches with respect to the way that habitats were classified. Bayer *et al.* (1991) classified the sites through Canonical Community Ordination (CANOCO; ter Braak, 1985) of environmental variables and relative abundance of community associates, whereas Brochmann & Elven (1992) categorised habitats based on relative importance of competition, stress and disturbance (Grime, 1988). The studies also differed in that Bayer *et al.* (1991) were studying apomictic polyploid *Antennaria rosea* Greene (Asteraceae), whereas those of Brochmann & Elven (1992) were amphimictic species of *Draba* L. (Brassicaceae).

Brochmann & Elven (1992) studied three diploid species of *Draba* and 13 of their allopolyploid derivatives (4x to 16x) from 443 populations in mainland Norway and Svalbard. The diploids were found to occur in stressful habitats (S-strategists, *sensu* Grime, 1988), whereas the majority of polyploids were stress tolerant competitors (CS-strategists *sensu* Grime, 1988) or ruderals (R-strategists, *sensu* Grime, 1988) (Brochmann & Elven, 1992). Most populations of the diploids, and populations of one polyploid, were found in heavily stressed habitats that were largely unvegetated. Six of the polyploid *Draba* species were classified as stress-tolerant competitors and occupy niches with moderate amounts of stress and competition, but usually low disturbance (Brochmann & Elven, 1992). Ruderals, occurring in disturbed sites, are represented by six other polyploids and occur on disturbed sites that may be either stressed or unstressed. All ploidy levels of the polyploids are represented in the stress tolerant competitors and ruderals. The ecological amplitude of each species was also evaluated using

the Shannon-Wiener index (Brochmann & Elven, 1992). They found that the diploids have very narrow ecological amplitude, but the polyploids have very wide ecological amplitude and occur across a large range of habitats with respect to stress, competition, and disturbance (Brochmann & Elven, 1992). Brochmann & Elven (1992) also investigated the association between ecological amplitude and genetic diversity (based on isozyme studies, Brochmann *et al.*, 1992c) and found a direct correlation between wide ecological amplitude and high amounts of genetic diversity expressed as heterozygosity.

Bayer *et al.* (1991) surveyed environmental variables and relative abundance of community associates at 101 sites occupied by the triploid/tetraploid gametophytic apomict *Antennaria rosea* and its putative progenitors. Each of the eight sexual species of *Antennaria* (L.) Gaertn., which are the diploid parents of *A. rosea*, appears to occur in a distinct habitat (Bayer *et al.*, 1991). These sexual species include *A. aromatica* Evert, *A. corymbosa* Nels., *A. marginata* E. Greene, *A. media* E. Greene /*pulchella* E. Greene, *A. microphylla* Rydb., *A. racemosa* Richards., *A. rosulata* Rydb., and *A. umbrinella*. Both community associates (the biotic factors) and environmental variables (the abiotic factors) can be used to predict which *Antennaria* species will occur in a given habitat and vice-versa (Bayer *et al.*, 1991). Some sympatric species pairs have similar habitats, although spatially overlapping or conterminous ones are uncommon (Bayer, Purdy & Lebedyk 1991). Habitat divergence tends to follow morphological divergence among the sexual taxa (Bayer, 1987). Those taxa that tend to be morphologically most distinct, such as *A. racemosa* and *A. marginata*, are also ecologically discrete (Bayer *et al.*, 1991). Habitat divergence among the species has obviously played an important role in the evolution of these species, as was suggested in Bayer (1987). Ecological isolation along with geographic isolation are the primary isolating mechanisms that help maintain species integrity and allow the species to continue to diverge (Bayer *et al.*, 1991).

The *A. rosea* sites occupy ordination space on the diagram (see Bayer *et al.*, 1991, figs. 5-7) that lies in the centre of the ordination and overlaps at least parts of those of all the sexual species except *A. aromatica* and *A. racemosa*. Several sites are, however, close to some of the *A. aromatica* sites. Many *A. rosea* sites do not occur in distinct habitats themselves, but instead occupy habitats that are very similar to those of their sexual progenitors (Bayer *et al.*, 1991). Some sites do fall in between the groups of sites of the sexual species and these habitats could be described as hybrid habitats since they have sets of conditions that are intermediate between or among groups of sexual taxa. None of the *A. rosea* sites cover the range of abiotic conditions associated with the sexual taxa, *i.e.*, they don't completely overlap the habitat of any of their sexual relatives (Bayer *et al.*, 1991). The CANOCO results support the hypothesis for the multiple hybrid origin of *A. rosea* proposed in Bayer (1990b), in that many sites of *A.*

rosea occupy similar habitats to their diploid progenitors, while others seem to occupy hybrid habitats that are intermediate between those of their sexual progenitors (Bayer *et al.*, 1991). The study of the ecology of *A. rosea* and its sexual relatives (Bayer *et al.*, 1991) illustrates that it is possible for the *Antennaria* species to come into contact to hybridise because their habitats overlap sporadically.

Levin's conclusion that polyploidy may drive a population into a new 'adaptive sphere', and allow it to occupy habitats that are beyond that of its progenitors (Levin, 1983) is supported by the results of this investigation. Polyploidy, particularly when accompanied by hybridisation between either different species or different ecotypes of the same taxon, is one of the quickest ways for new species or races to become adapted to different ecological circumstances (Stebbins, 1984). This is supported by both the *Antennaria* and *Draba* studies (Bayer *et al.*, 1991; Brochmann & Elven, 1992).

Ehrendorfer (1980) has suggested that in established floras polyploidy contributes intermediate 'fill-in' taxa that contribute to a more intensive partitioning of areas and eventually leads to a saturation of most available habitats by the progenitor taxa and their polyploid derivatives. This may be the most significant adaptive role that polyploidy performs. *Antennaria rosea* seems to fulfil this prediction in that many *A. rosea* populations exist in habitats that are both unoccupied by and intermediate to those of its progenitors. On the other hand, *Draba* polyploids seem to occupy habitats that are not in any way intermediate between the diploids, but a gradient of which only one extreme represents the niche space of the diploids (Brochmann & Elven, 1992). It could be that sexual polyploid *Draba* have diverged significantly in a relatively short amount of time to be able to colonise novel habitats in the arctic environment, whereas the apomictic *A. rosea* is limited to sites that are similar to their parents or intermediate between them.

Conclusions

New molecular approaches provide us with powerful new tools to investigate the evolution of polyploids. Clearly, many old ideas about polyploidy, such as the frequency of formation of polyploids and relative numbers of autopolyploids vs. allopolyploids, will need re-evaluation given new molecular evidence.

A number of new findings have been presented here, but these studies are just the beginning of what hopefully will lead to more investigations along similar avenues. One of the most important recent findings to the evolution of polyploidy is that significant chromosomal repatterning occurs in the amphidiploids subsequent to their formation and that this can take place within a very few generations. Molecular studies are not the only ones that will make a substantial contribution to our knowledge of the

evolution of polyploidy. Ecological studies, which allow us to study the response of polyploids and agamosperms to their environment, will help us learn more about the adaptive significance of polyploidy and apomixis. Clearly, there is a difference in habitat preference by diploids and tetraploids, although the difference in niche preference by different polyploid levels is less clear. There may be a direct correlation between wide ecological amplitude and high amounts of genetic diversity in the polyploids. Balanced polymorphism for cytotypes, as seen in the autopolyploids in *Andropogon gerardi*, may be adaptive because it can extend the ecological amplitude of the species. Intraspecific polyploidy, as a form of genetic variation, is worthy of future investigation.

The adaptive significance of polyploidy, with respect to both sexual and agamic complexes, is that it may allow the polyploids to occupy niche space not occupied by their diploid progenitors, whether they are in intermediate habitats or divergent habitats to the diploids. In agamic complexes, such as are seen in some species of *Antennaria*, dynamic populations exist that are complex mixtures of sexuals, facultative apomicts, and obligate apomicts. The adaptive significance of the balance among these reproductive strategies is uncertain, but it seems likely that the facultative apomicts are responsible for the generation of new obligate apomicts to be tested by natural selection. More research is needed in all of these areas before solid statements concerning the early evolution and adaptive significance of polyploidy can be made.

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