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POLYPLOIDY AND SELF-FERTILIZATION IN FLOWERING PLANTS[1]

BRIAN C. BARRINGER[2]

Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, New York 14853 USA

Mating systems directly control the transmission of genes across generations, and understanding the diversity and distribution of mating systems is central to understanding the evolution of any group of organisms. This basic idea has been the motivation for many studies that have explored the relationships between plant mating systems and other biological and/or ecological phenomena, including a variety of floral and environmental characteristics, conspecific and pollinator densities, growth form, parity, and genetic architecture. In addition to these examples, a potentially important but poorly understood association is the relationship between plant mating systems and genome duplication, i.e., polyploidy. It is widely held that polyploid plants self-fertilize more than their diploid relatives, yet a formal analysis of this pattern does not exist. Data from 235 species of flowering plants were used to analyze the association between self-fertilization and ploidy. Phylogenetically independent contrasts and cross-species analyses both lend support to the hypothesis that polyploids self-fertilize more than diploids. Because polyploidy and self-fertilization are so common among angiosperms, these results contribute not only to our understanding of the relationship between mating systems and polyploidy in particular, but more generally, to our understanding of the evolution of flowering plants.

Key words: angiosperms; comparative analysis; flowering plants; inbreeding depression; mating systems; phylogenetically independent contrasts; polyploidy; self-fertilization.

The diversity and distribution of mating systems in plants have been of longstanding interest, and it is widely acknowledged that mating systems can profoundly influence the evolutionary trajectories and long-term success of taxa (Darwin, 1859, 1876; Stebbins, 1950, 1957; Grant, 1981, Lande and Schemske, 1985; Barrett and Eckert, 1990; Barrett et al., 1996; Barrett, 2003). Because mating systems are influenced and molded by environmental and genetic factors (Barrett and Eckert, 1990; Barrett, 2003), they are not simply static descriptors of a taxon's life history, but are, rather, dynamic and evolving traits in and of themselves (Barrett and Eckert, 1990). For these reasons, a thorough understanding of the evolution of plant mating systems and the patterns of their distributions is clearly fundamental to an understanding of the evolution of flowering plants.

Some of the most persistent questions surrounding the evolution of plant mating systems are those that address the evolution of self-fertilization. In the absence of pollen discounting (the reduction due to selfing in the number of pollen grains available for outcrossing [Harder and Wilson, 1998]), selfing is advantageous because a selfing individual will pass on two copies of its genome for every copy passed on by an outcrossing individual (Fisher, 1941). This "cost of outcrossing" provides a 50% fitness advantage to selfing variants in otherwise outcrossing populations, and unless counteracted by some other selective force, will translate to increased population selfing rates (Fisher, 1941; Charlesworth and Charlesworth, 1979). In addition, self-fertilization may be advantageous as a reproductive assurance mechanism (Stebbins, 1950, 1957; Grant, 1981; Pannell and Barrett, 1998; Morgan and Wilson, 2005) or as a means of fixing co-adapted gene complexes (Lande and Schemske, 1985).

In contrast to phenomena that might favor the evolution of selfing are a variety of factors that may select for outcrossing, such as pollen discounting (Harder and Wilson, 1998), temporal and spatial variation in environmental conditions (Maynard-Smith, 1978; Lande and Schemske, 1985), and tradeoffs in the allocation of energy to male and female functions resulting in gender specialization (Charnov et al., 1976; Brunet, 1992; Thomson, 2006). In addition, inbreeding depression (the reduction in fitness of inbred relative to noninbred individuals) is often hypothesized to be strong enough to overcome the selective cost to outcrossing (Charlesworth and Charlesworth, 1979, 1987; Lande and Schemske, 1985; Husband and Schemske, 1996, 1997). If inbreeding depression leads to a 50% fitness reduction in selfed progeny relative to outcrossed siblings, selfing may no longer be advantageous (Charlesworth and Charlesworth, 1979, 1987; Lande and Schemske, 1985; but see Holsinger, 1988). Despite the detrimental effects of inbreeding and the potential benefits of outcrossing, high levels of self-fertilization have evolved repeatedly in many groups (Stebbins, 1950; Johnston and Schoen, 1996).

The transition from outcrossing to selfing in plants is correlated with many biological and ecological phenomena, including a variety of floral and environmental characteristics, conspecific and pollinator densities, growth form, parity, and genetic architecture (Darwin, 1876; Stebbins, 1950, 1957; Grant, 1956, 1981; Charlesworth and Charlesworth, 1979; Wyatt, 1984; Lloyd, 1992; Barrett et al., 1996; Pannell and Barrett, 1998; Morgan, 2001; Barrett, 2003; Morgan and Wilson, 2005; Scofield and Schultz, 2006). In addition to these

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[2] E-mail: bcb24@cornell.edu, phone: 607-254-4282, fax: 607-255-8088

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examples, a potentially important though poorly understood association is the relationship between self-fertilization and genome duplication, i.e., polyploidy. Polyploids are organisms with more than two sets of chromosomes (Grant, 1981; Soltis et al., 2004), and, although relatively rare in most groups of animals (Otto and Whitton, 2000; Mable, 2004b; but see Legatt and Iwama, 2003), polyploidy is common in flowering plants (Soltis et al., 2004). The relationship between polyploidy and self-fertilization in plants has been of interest for many years, because it is widely held that polyploids have higher selfing rates than their diploid relatives (Stebbins, 1950; Mable, 2004a). There are several nonmutually exclusive reasons why polyploidy might be associated with increased levels of selfing in plants: first, polyploidy may facilitate the evolution of self-fertilization because it results in a breakdown of self-incompatibility (SI) systems in many groups of plants, especially those whose SI systems are gametophytic (Bateman, 1952; Barrett, 1987; Mable, 2004a). Because SI systems reduce or eliminate the ability to self-fertilize, it follows that some polyploids may have increased levels of selfing compared to their diploid relatives whose SI systems remain intact. Second, the ability to self-fertilize may facilitate the evolution of polyploidy. Newly arisen polyploids (i.e., *neo*polyploids) are likely to co-occur with their diploid progenitors (Levin, 1975; Jackson, 1976; Ramsey and Schemske, 1998), and because intercytotype crosses often result in offspring with low fitness (Levin, 1975; Ramsey and Schemske, 1998), minority cytotypes are expected to experience negative frequency-dependent selection, a phenomenon referred to as minority cytotype disadvantage (Levin, 1975). The ability to self-fertilize should reduce the effects of minority cytotype disadvantage by eliminating the need for a cytoplasmically compatible mate, and for this reason it may be that selfing taxa, on average, successfully produce more polyploids than do outcrossing taxa (Grant, 1956, 1981; Stebbins, 1957; Levin, 1975; Ramsey and Schemske, 1998). Finally, some theoretical work predicts that polyploids may exhibit less inbreeding depression than diploids, owing to the presence of multiple gene copies and the associated reduction in the rate of formation of homozygotes (Lande and Schemske, 1985). The relationship between polyploidy and inbreeding depression is complex, however, and levels of inbreeding depression in polyploids have been shown to depend on many additional factors, including the level of dominance of deleterious alleles, the number and lethality of genes involved, and the age of the polyploid in question (Ronfort, 1999; Pannell et al., 2004; Rausch and Morgan, 2005). Indeed, some studies predict that, under some circumstances, polyploids might exhibit greater inbreeding depression than their diploid relatives (Busbice and Wilsie, 1966; Bennett, 1976; Ronfort, 1999). In addition, polyploids differ in regard to the behavior of their chromosomes during cell division, and although *auto*polyploids (polyploids that possess only homologous chromosomes) may effectively mask deleterious alleles better than diploids, *allo*polyploids (polyploids that possess homeologous chromosomes) are expected to have chromosomal behavior similar to that of diploids and may not exhibit increased tolerance to inbreeding (Bever and Felber, 1992; Ronfort, 1999; Soltis and Soltis, 2000; Comai, 2005). To date, theoretical work has concentrated on autopolyploids, however, and no formal theoretical explorations of inbreeding depression in allopolyploids exist (Pannell et al., 2004; but see Lande and Schemske, 1985). Comparative data on inbreeding depression in closely related polyploid and diploid taxa are few (Ramsey and Schemske, 2002; Pannell et al., 2004), but at least two studies indicate lower inbreeding depression in autopolyploids relative to diploids (Husband and Schemske, 1997; Rosquist, 2001). The ability to increase levels of selfing without suffering the detrimental consequences of inbreeding depression should select for increased selfing rates among polyploids.

Despite increasing interest in the evolution of both polyploidy and plant mating systems, surprisingly few studies have carefully evaluated whether polyploids do, in fact, self-fertilize more than diploids (Ramsey and Schemske, 1998; Mable, 2004a). Among homosporous ferns, polyploids do tend to self-fertilize more than diploids (Soltis and Soltis, 1987, 1990; Masuyama and Watano, 1990), and very limited support for this trend in gymnosperms also exists (B. C. Barringer, unpublished data). Whether this pattern holds across the angiosperms remains unknown, however, despite many anecdotal examples (e.g., Stebbins, 1950; Grant, 1956, 1981). One way to answer this question would be to compare the mating systems of polyploid angiosperms and their immediate progenitor taxa (i.e., sister-taxon comparisons); the relationships between polyploids and their progenitors are often unknown, however, and selfing rates for those groups in which such relationships are known have generally not been estimated (Husband and Schemske, 1997). Both Stebbins and Grant describe several genera (e.g., *Amsinckia, Bromus, Clarkia, Gilia, Microseris*) wherein polyploids self more than diploids (Stebbins, 1950; Grant, 1956, 1981), and others have since documented this trend within specific groups (Ross, 1981; Husband and Schemske, 1997; Cook and Soltis, 2000; Quarin et al., 2001; Tate and Simpson, 2004; Guggisberg et al., 2006). The opposite pattern occurs among diploid and polyploid species of *Tragopogon* (Asteraceae) (Cook and Soltis, 1999), however, and although polyploidy might generally be associated with a loss or breakdown of gametophytic SI systems, a recent review failed to find a widespread association between polyploidy and self-compatibility, especially among taxa with sporophytic or heteromorphic SI (Mable, 2004a). Finally, although polyploidy has resulted in a breakdown of SI in the genus *Lycium* (Solanaceae), this may have led to an increase in inbreeding depression as rates of self-fertilization increased, which facilitated selection for higher outcrossing rates among polyploids via the evolution of gender dimorphism (Miller and Venable, 2000).

Here I examine the association between ploidy and self-fertilization using data from 235 species of flowering plants for which levels of self-fertilization have been estimated. I report results from two separate analyses of these data: (1) phylogenetically independent contrasts (PICs), which control for phylogenetic relationships among taxa, and (2) an analysis that does not control for phylogeny but instead treats each species as an independent data point (i.e., cross-species analysis). In each analysis I ask whether polyploids have higher levels of self-fertilization than diploids. Annuals, herbaceous perennials, and woody perennials differ in their average rates of self-fertilization (Barrett and Eckert, 1990; Barrett et al., 1996). Accordingly, these three life-history categories are represented by an additional independent variable (along with ploidy) in the second analysis (cross-species analysis). In addition, the relationship between polyploidy and self-fertilization might differ among major groups of angiosperms; therefore, in both analyses the monocotyledons, rosids, and asterids were analyzed on their

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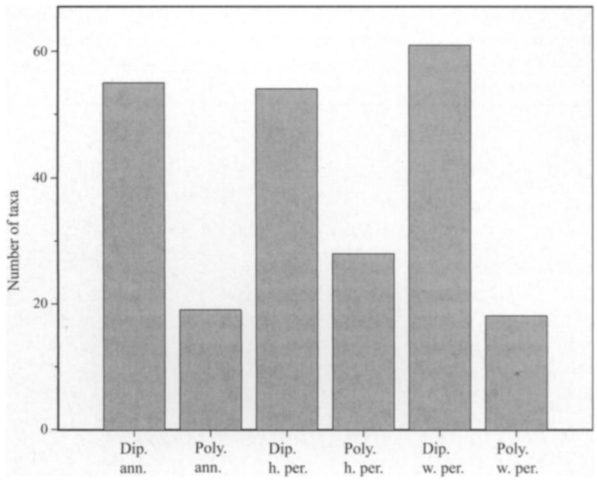

Fig. 1. Numbers of taxa represented in the data set by diploid annuals (Dip. ann.), polyploid annuals (Poly. ann.), diploid herbaceous perennials (Dip. h. per.), polyploid herbaceous perennials (Poly. h. per.), diploid woody perennials (Dip. w. per.), and polyploid woody perennials (Poly. w. per.).

own in addition to the analysis of the entire data set. Although within-family comparisons might be a more informative and/or biologically meaningful way to analyze angiosperm life-history data, most families included in this study lack variation in ploidy (among those species represented in the data set), making within-family comparative analysis impossible.

MATERIALS AND METHODS

Selfing rate and ploidy database—Selfing rate estimates for angiosperm taxa were compiled from the primary literature. S. C. H. Barrett and C. G. Eckert provided a database of selfing rates from studies published through 1995 (S. C. H. Barrett, University of Toronto, and C. G. Eckert, Queen's University, personal communication). I gathered additional data on selfing rates published since 1995 (through March 2006) using the *Science Citation Index Expanded* (ISI Web of Knowledge, Web of Science, Science Citation Index Expanded, 1900–2007) online science literature database. Only levels of selfing measured in natural populations (i.e., occurring in their natural habitat and range) were included. Because most studies report population outcrossing rates, the selfing rate for a given study population is equal to $1 - t$, where t is the outcrossing rate. For studies reporting estimates of $t > 1$ (which may occur if multiple loci are used and one or more assumptions of the model used to estimate outcrossing rates are violated [Ritland and Jain, 1981]), the selfing rate was set to zero. For some taxa, levels of self-fertilization have been estimated for multiple populations and/or for the same population during multiple years. If multiple estimates of t were available for a species, I used the mean value of the estimates in my analyses.

Chromosome numbers for most taxa were obtained from the Missouri Botanical Garden's Index to Plant Chromosome Numbers (http://mobot.mobot.org/W3T/Search/ipcn.html) or the Chromosome Atlas of Flowering Plants (Darlington and Wylie, 1955). For a few species (6%), taxon-specific literature was consulted for chromosome counts not reported in these sources. Because information on ploidy does not exist for most species, I inferred relative ploidy levels for individual taxa by comparing basal chromosome numbers for a given genus (Darlington and Wylie, 1955) to those reported for the species in question (sensu Mable, 2004a). Darlington and Wylie (1955) defined basal chromosome numbers as the largest common denominator of all published chromosome counts for a given genus. Taxa with chromosome numbers that are two times the basal number are treated as diploids, while those with more than two times the basal number are treated as polyploids.

The complete data set (Appendix S1, see Supplemental Data accompanying the online version of this article) contains 235 species of flowering plants from 126 genera and 58 families (Cronquist, 1981, 1988; APG Angiosperm Phylogeny Group, 2003), and includes 170 diploids and 65 polyploids. There are 74 annuals, 82 herbaceous perennials, and 79 woody perennials in the data set. The numbers of diploids and polyploids in each of the three life-history categories are shown in Fig. 1.

Statistical analyses—Selfing rate data were arcsine ($\sqrt{y}$) transformed before analysis to better meet assumptions of normality/equal variance. Normality was assessed using Minitab (version 13.1, Minitab Inc., State College, PA, USA) and a Ryan-Joiner normality test ($r = 0.9819$, $P = 0.0710$). Homogeneity of variance was assessed using Minitab and a Levene test ($L = 1.127$, $P = 0.341$). For all analyses, results from the analysis of nontransformed data were qualitatively the same.

Analysis 1 (phylogenetically independent contrasts)—Because plant mating systems are distributed nonrandomly with respect to phylogeny (Barrett and Eckert, 1990), PICs were constructed to control for phylogenetic relations among taxa (Felsenstein, 1985). The MacClade software package (Maddison and Maddison, 1992) was used to build a phylogenetic tree (MacClade file available from the author on request) containing all of the 235 species in the data set, based on the Davies et al. (2004) phylogeny of flowering plants. Taxon-specific literature was used to resolve relationships within families, but several genus- and species-level polytomies remain in the finished tree, owing to a lack of available data for some groups. The Comparative Analysis by Independent Contrasts (CAIC) software package (Purvis and Rambaut, 1995) was then used to identify and calculate PICs for four different trees: (1) the entire tree containing all 235 species, (2) a tree that included monocotyledons only (43 species), (3) a tree that included rosids only (92 species), and (4) a tree that included asterids only (77 species). All branch lengths were set equal; results from the analysis of trees for which branch lengths had been estimated using the algorithm described by Grafen (1989) were qualitatively the same. CAIC uses one of two different models to calculate PICs: CRUNCH (if all variables in the analysis are continuous) or BRUNCH (if the analysis includes one or more categorical variables) (Purvis and Rambaut, 1995). Because ploidy is categorical, the BRUNCH model was used. When performing PICs, CAIC automatically investigates potential violations in the assumptions of regression analysis (http://www.bio.ic.ac.uk/evolve/software/caic/assumptions.html); no violations were found.

Analysis 2 (cross-species analysis)—Shifts between outcrossing and selfing as well as changes in ploidy are very common among angiosperms (Barrett et al., 1996; Soltis et al., 2004), and because mating systems and ploidy are evolutionarily labile (relative to rates of speciation), phylogenetic correction may not be necessary (Felsenstein, 1985; Westoby et al., 1995; Barrett et al., 1996; Ricklefs and Starck, 1996; Price, 1997; Larson and Barrett, 2000; Rheindt et al., 2004) (see Discussion). In addition, levels of self-fertilization among flowering plants correlate strongly with life history; annuals tend to self more than herbaceous perennials, which in turn have higher selfing rates than woody perennials (Barrett and Eckert, 1990; Barrett et al., 1996). Therefore, for the cross-species analysis, I included both ploidy and life history (and their interaction) as independent variables in a two-way analysis of variance (ANOVA) using PROC GLM in SAS (SAS Institute, 1999–2001). As in analysis 1, the monocotyledons, rosids, and asterids were analyzed separately in addition to the overall analysis, which included all 235 species in the data set.

RESULTS

Analysis 1 (phylogenetically independent contrasts)—The CAIC program identified 32 PICs from among the 235 species represented in the complete phylogeny, and the mean contrast value is significantly greater than zero, indicating that polyploids tend to have higher levels of selfing than their diploid relatives ($N = 32$ contrasts, $P = 0.0011$) (Table 1, Fig. 2). When analyzed on their own, monocotyledons ($N = 9$ contrasts, $P = 0.0274$) and rosids ($N = 11$ contrasts, $P = 0.0013$) also exhibit higher levels of selfing among polyploids than among diploids. In contrast, the asterids provide no support for the hypothesis that polyploidy is associated with

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TABLE 1. Phylogenetically independent contrasts. Positive contrast values indicate higher selfing rates among polyploids relative to diploids.

Analysis	No. taxa	No. contrasts	No. positive	*P*
All species	235	32	22	0.0011
Monocotyledons only	43	9	7	0.0274
Rosids only	92	11	10	0.0013
Asterids only	77	7	3	0.6255

increased levels of self-fertilization ($N = 7$ contrasts, $P = 0.6255$).

Analysis 2 (cross-species analysis)—When all 235 species are treated as independent data points, polyploids have significantly higher levels of selfing than diploids ($N = 235$, $P = 0.0001$) (Table 2). Results from the other three cross-species analyses are similar: monocotyledons ($N = 43$, $P = 0.0067$), rosids ($N = 92$, $P = 0.0143$), and asterids ($N = 77$, $P = 0.0112$). In addition, life history correlates strongly with selfing rate in all four cross-species analyses, with annuals having higher levels of selfing than herbaceous perennials, which in turn have higher levels of selfing than woody perennials. The interaction between ploidy and life history was nonsignificant for all four analyses. The distribution of selfing rates for all six possible combinations of ploidy and life history are shown in Fig. 3, and the least-squares mean selfing rates for diploids and polyploids and for annuals, herbaceous perennials, and woody perennials are shown in Tables 3 and 4, respectively.

DISCUSSION

This study is the first to analyze the relationship between polyploidy and self-fertilization in flowering plants in a phylogenetic context using quantitative estimates of selfing rates from natural populations. As indicated by phylogenetically independent contrasts and cross-species analysis, polyploid angiosperms tend to have higher rates of self-fertilization than their diploid relatives. This trend is not apparent in the asterids when PICs are used, but there are only seven PICs in the asterid phylogeny, and the lack of power in this analysis may be exacerbated by a relatively low level of phylogenetic resolution among the asterids than among the other phylogenetic trees used in this study. Polytomies can reduce the validity and power of CAIC, and cross-species analysis can be more powerful than PICs when a phylogenetic tree is fairly unresolved (Purvis and Rambaut, 1995). In addition, although studies suggest that polyploidy is generally associated with a

TABLE 2. Analysis of variance on the effects of ploidy, life history, and their interaction on selfing rate in the cross-species analysis.

Analysis	df	Type III SS	F	*P*
All species				
Ploidy	1	1.25	15.30	0.0001
Life history	2	4.33	26.61	<0.0001
Ploidy × life history	2	0.22	1.35	0.2607
Error	229	18.65		
Monocotyledons only				
Ploidy	1	0.98	8.21	0.0067
Life history	1	0.82	6.90	0.0122
Ploidy × life history	1	0.11	0.96	0.3333
Error	39	4.64		
Rosids only				
Ploidy	1	0.37	6.26	0.0143
Life history	2	0.88	7.43	0.0011
Ploidy × life history	2	0.12	0.96	0.3855
Error	86	5.11		
Asterids only				
Ploidy	1	0.60	6.78	0.0112
Life history	2	1.07	6.08	0.0037
Ploidy × life history	2	0.06	0.34	0.7130
Error	71	6.27		

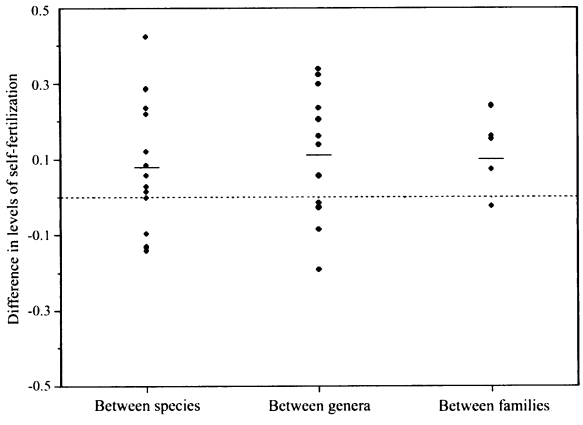

Fig. 2. Differences in levels of self-fertilization between diploids and polyploids for each of the 32 phylogenetically independent contrasts, arranged in three groups according to node depth (between species, between genera, and between families). For a given contrast, a positive value indicates higher levels of selfing in polyploids relative to diploids, while a negative value indicates the reverse. For each group, a solid line indicates the mean contrast value.

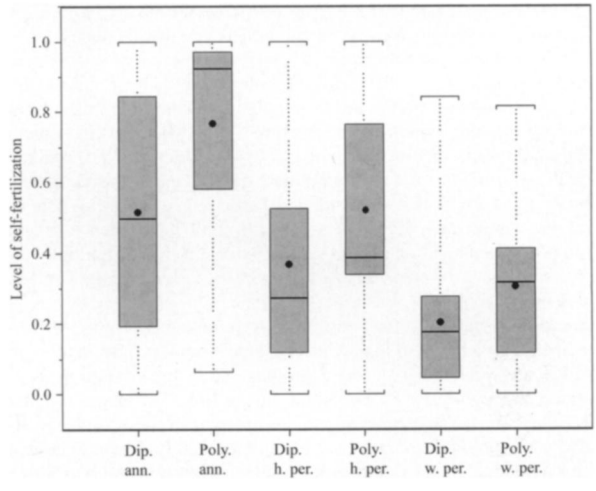

Fig. 3. Levels of self-fertilization for diploid annuals (Dip. ann.), polyploid annuals (Poly. ann.), diploid herbaceous perennials (Dip. h. per.), polyploid herbaceous perennials (Poly. h. per.), diploid woody perennials (Dip. w. per.), and polyploid woody perennials (Poly. w. per.). For each group, the central bar indicates the median value, the filled circle indicates the mean value, the shaded box represents the interquartile range, and the dashed line indicates the total range.

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TABLE 3. Least-squares means of selfing rates in the cross-species analysis for diploids and polyploids. Values in parentheses indicate standard errors. For each data set used, means were significantly greater for polyploids than for diploids (Tukey–Kramer honestly significant difference, for $\alpha = 0.05$).

Analysis	Diploids	Polyploids
All species	0.36 (0.02)	0.53 (0.04)
Monocotyledons only	0.41 (0.07)	0.76 (0.10)
Rosids only	0.43 (0.03)	0.60 (0.06)
Asterids only	0.33 (0.05)	0.54 (0.06)

TABLE 4. Least-squares means of selfing rates in the cross-species analysis for annuals, herbaceous (herb.) perennials (per.), and woody perennials. Values in parentheses indicate standard errors. Different superscripts within rows indicate means that differ significantly (Tukey–Kramer honestly significant difference, for $\alpha = 0.05$).

Analysis	Annuals	Herb. per.	Woody per.
All species	0.64 (0.04)[a]	0.43 (0.03)[b]	0.25 (0.04)[c]
Monocotyledons only	0.74 (0.10)[a]	0.43 (0.07)[b]	na
Rosids only	0.66 (0.06)[a]	0.55 (0.06)[a]	0.34 (0.06)[b]
Asterids only	0.61 (0.06)[a]	0.41 (0.07)[a,b]	0.27 (0.08)[b]

Note: na = not applicable

breakdown in gametophytic SI systems (Mable, 2004a), there is no evidence for a ploidy-dependent breakdown of SI in the Asteraceae (S. Good-Avila, Acadia University, personal communication). Of the 77 taxa analyzed in the asterid clade, 29 (38%) belong to the Asteraceae, and this may further explain the lack of evidence for increased selfing rates among polyploid asterids.

Selfing rates appear to evolve rapidly relative to rates of speciation in flowering plants (Barrett et al., 1996), and floral traits associated with selfing (e.g., small petal size, simultaneous maturation of pollen and receptivity of stigma, and close spatial proximity of anther and stigma) often differ among subspecies and populations (Wyatt, 1984). For example, the two subspecies of *Clarkia xantiana* have markedly different breeding systems (Runions and Geber, 2000), and both *C. exilis* and *C. tembloriensis* have high variation in selfing rates among populations (Vasek and Harding, 1976; Holtsford and Ellstrand, 1989). Both genetic and environmental factors contribute to the evolution of mating systems in plants (Barrett and Eckert, 1990; Barrett, 2003), and rates of self-fertilization are known to change rapidly (relative to rates of speciation) in response to a changing environment (Stebbins, 1950, 1957; Grant, 1981; Schemske and Lande, 1985; Barrett and Eckert, 1990; Barrett et al., 1996; Barrett, 2003). Because plant mating systems are so evolutionarily labile, it could be argued that controlling for phylogenetic relations among taxa may be unduly conservative in this study. Indeed, a similar argument might be applied to changes in ploidy because chromosome number varies among populations of many species (Grant, 1981; Otto and Whitton, 2000; Soltis et al., 2004) and changes in chromosome number are not necessarily related to speciation events. Because life-history traits are often phylogenetically constrained (Mazer, 1990; Peat and Fitter, 1994; Moles et al., 2005), however, it is possible that phylogenetic inertia of traits not included in this study could contribute to differences in selfing rates and/or differences in ploidy. This possibility justifies controlling for phylogenetic relationships among the taxa analyzed here.

As shown in Table 2, the effect of the interaction between ploidy and life history on levels of self-fertilization was nonsignificant in all four of the cross-species analyses, indicating that the relationship between ploidy and self-fertilization does not depend on life history. Annuals, herbaceous perennials, and woody perennials all tend to have increased selfing rates among polyploids relative to diploids. As can be seen in Fig. 3, however, levels of self-fertilization range widely in all categories regardless of ploidy or life history, suggesting that selective forces not considered in this study influence the evolution of self-fertilization. In agreement with previous studies (Barrett and Eckert, 1990; Barrett et al., 1996), selfing rates are negatively associated with life history, and this trend is apparent in both polyploids and diploids. Annual species have higher selfing rates than perennials. Among perennials, herbaceous species self more than relatively long-lived woody species. This result is consistent with theoretical expectations that short-lived species should tend to self-fertilize more than long-lived species, owing to selection for reproductive assurance in the former (Stebbins, 1950) and the cost of seed discounting (decreasing levels of outcrossed seed production due to increased levels of self-fertilization) in the latter (Lloyd, 1992; Morgan et al., 1997). There are other reasons why outcrossing rates might be higher in long-lived species as well. For example, long-lived species (e.g., trees and shrubs) are often larger than short-lived species (e.g., herbs), and because plant cells are not differentiated into distinct somatic and germ cell lineages, mutations that occur during mitosis can contribute to the genetic load carried by gametes. Because larger plants are expected to have a greater number of mitotic cell divisions between germination and the production of gametes (relative to smaller plants), this may lead to profound inbreeding depression and strong selection against selfing (Morgan, 2001; Scofield and Schultz, 2006).

Polyploids are known to undergo diploidization, a process by which their chromosomal behavior reverts back to that of a diploid, owing to a variety of phenomena such as large-scale genomic rearrangements, gene silencing and/or loss, and the evolution of novel functions by one or more copies of duplicated genes (Wendel, 2000; Wolfe, 2001; Soltis et al., 2004). Though some taxa treated as polyploids in this study may behave cytogenetically as diploids, the methods used ensure that such taxa have undergone a relatively recent polyploidization event because they were compared to congeners possessing at least half as many chromosomes. The assumption then is that the evolution of self-fertilization might be associated with polyploidization regardless of the current cytogenetic behavior of a given taxon.

Allopolyploids may not differ from diploids in terms of inbreeding depression (Bever and Felber, 1992; Ronfort, 1999; Soltis and Soltis, 2000; Comai, 2005), and if decreased inbreeding depression contributes to the evolution of higher selfing rates among polyploids, it would be of interest to know whether this pattern occurs in both allo- and autopolyploids, or is more prevalent in one group relative to the other. Unfortunately, the category of ploidy is not known for the majority of polyploids included in this study, and whether allo- and autopolyploids differ in terms of their relationship with self-fertilization remains unknown. Autopolyploids were once thought to be quite rare (Grant, 1981), but there is growing evidence that they are much more common in nature than

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initially believed (Soltis et al., 2004). Because most theoretical and empirical work has focused on autopolyploidy and its effects on the evolution of self-fertlization (e.g., Husband and Schemske, 1997; Ronfort, 1999; Rausch and Morgan, 2005), the results presented here suggest that either autopolyploids are indeed more common (at least among those polyploids represented in the data set) or that the association between self-fertilization and polyploidy does not differ between allo- and autopolyploids.

Conclusions—In agreement with other studies (e.g., Cook and Soltis, 2000; Quarin et al., 2001; Tate and Simpson, 2004; Guggisberg et al., 2006), the data support the hypothesis that polyploid angiosperms have, on average, higher rates of self-fertilization than their diploid relatives. Of continued interest are the evolutionary and ecological phenomena that underlie this pattern, and they are likely both numerous and varied. The ability to self-fertilize may increase the likelihood that newly arisen polyploids can establish successful populations, and selfing taxa may give rise to successful polyploid lineages more often than do outcrossing taxa. Decreased levels of inbreeding depression in polyploids might also help to explain why polyploids have higher rates of self-fertilization than diploids. The relationship between ploidy and inbreeding depression is complex, however, and has been shown to depend on many factors, including the number and lethality of deleterious alleles, the degree of dominance among alleles and epistasis among loci, and the age of the polyploid in question (Ronfort, 1999; Pannell et al., 2004). More empirical studies that compare mating systems and inbreeding depression in closely related polyploids and diploids are needed to further address these issues. In addition, auto- and allopolyploids may differ in their response to inbreeding. Accordingly, models that compare and explore further the evolution of inbreeding depression in polyploids and diploids—especially those that differentiate between neopolyploids vs. older polyploids and autopolyploids vs. allopolyploids—will be of value.

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