

# Pollination, Floral Display, and the Ecological Correlates of Polyploidy

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## ABSTRACT

Polyploidy is recognized as having a significant impact on plant evolution, with estimates of half of all vascular plants being of polyploid origin. It was first suggested in the 1940's that polyploid species are concentrated in perennial herbs and in northern, temperate climates. Since then, there has been further attention concentrated on the ecological correlates of polyploidy, with an emerging interest in how polyploidization influences the pollination of a species. Here, we highlight recent work in pollination dynamics subsequent to polyploidization and gather information on differences in flower display characters between polyploids versus diploids. We posit that more thorough study of the effects of polyploidization on floral display is required, as this sub-field potentially provides keen insights into when and where polyploidy may be favoured via its effects on pollen delivery. Furthermore, our review of the evidence reveals that correlations between polyploidy and floral display in terms of flower size and flower number may influence perceived correlations between polyploidy and self-compatibility.

**Keywords:** floral display, macroecology, polyploidy, pollination, self-compatibility

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## INTRODUCTION

Polyploidization is arguably the most pervasive process in plant evolution, with perhaps over half of all vascular plants being of polyploid origin (Grant 1971; Haufler 1987; de Bodt *et al.* 2005). Various aspects of polyploidy have occupied plant systematists-evolutionists for decades (Stebbins 1971, 1980; Soltis and Soltis 1993). Because polyploidy is such a dominant feature of flowering plant genomes, it has been argued that polyploidy confers evolutionary advantages to plant species and has provided opportunities for different ecological interactions (herbivory, pollination), which have resulted in an increase in biodiversity (Thompson *et al.* 1997; Otto and Whitton 2000; Thompson *et al.* 2004; Thompson and Whitton 2006). Because pollination dynamics figure heavily into the diversification of angiosperms as well (e.g. Perez *et al.* 2006; van der Niet *et al.* 2006), it is perhaps surprising that the connection between pollination and polyploidy has received so little direct attention. Here, we review the ecological and mating system correlates of polyploidy and how these correlates may influence, and be influenced by, the effect of polyploidization

on pollinator dynamics.

Sexual system persists as one of the most important traits contextualizing the establishment and maintenance of polyploid lineages (Pannell *et al.* 2004). It is widely speculated that polyploidy should be strongly correlated with self-compatibility for two reasons. First, the process of genome doubling may disrupt self-incompatibility mechanisms that are maintained in the diploid state (Miller and Venable 2000), and polyploids should exhibit increased immunity to the negative effects of inbreeding depression due to the presence of multiple gene copies (Lande and Schemske 1985; Otto and Whitton 2000). Although this latter point has been disputed (Busbice and Wilsie 1966; Bennett 1976), the expectation becomes that transitions to polyploidy should often be concurrent with transitions to increased self-compatibility and higher selfing rates. Second, neopolyploids are generally the minority cytotype in the population and thus outcrossers are more likely to encounter the gametes of their diploid progenitors. This leads to a disadvantage because resulting offspring are often triploids, which tend to have reduced fertility compared to those of even ploidy. Self-compatible polyploids can avoid this minority cytotype dis-

advantage by producing polyploid, self-fertilized offspring. Therefore, polyploid cytotypes that arise within self-compatible lineages, or increase in self-compatibility upon polyploidization, should be more likely to persist than those that arise in self-incompatible lineages and maintain their self-incompatibility. Early studies supported the prediction that polyploidy is correlated with self-compatibility (Crane and Lewis 1942; Hecht 1944; Lewis 1947; Williams 1951; Bateman 1952). However, a recent, comprehensive between-species analysis refutes the existence of a strong, widespread association between self-compatibility and ploidy level between species (Mable 2004). Nonetheless, this result is not inconsistent with the theoretical prediction described above, since between-species comparisons do not necessarily reflect transient trait values immediately prior to or following polyploidization. Self-compatibility could be selected in neopolyploids due to reduced minority cytotype disadvantage and reduced inbreeding depression; but as substantial pre-mating reproductive isolation builds up between diploids and polyploids, perhaps facilitated by functional divergence between duplicate gene copies, the selection for strong self-compatibility could decrease or reverse. Likewise, although polyploidization may in some cases cause a disruption of self-incompatibility mechanisms, this does not preclude the possibility that self-incompatibility could be reestablished over the longer term, especially when self-compatibility is intermediate and/or variable between genotypes (Mable 2004). Therefore, although there is at best only weak evidence that self-compatibility is more common in contemporary polyploid species, self-compat-

ibility may nevertheless be more common in polyploid cytotypes or young polyploid species collectively (hereafter collectively referred to as neopolyploids).

The conflicting evidence over self-compatibility and polyploidy may also suggest another important factor at play during polyploidization, likely a factor that is related to both mating system and polyploidy. The pollination system is a strong candidate in this regard, since this is a factor of global importance, with known relationship to both mating system and fitness. Considering the longstanding interest in mating system and polyploidy, and the widely recognized relationships between mating systems, pollination mechanisms, and floral display traits, there has been a surprising lack of attention paid to floral display and the pollination of polyploid cytotypes and species. Self-compatibility is expected to be common in neopolyploids; but additionally, selfing species often have relatively small, inconspicuous flowers and low pollen-to-ovule ratios (Cruden and Lyon 1985; Cruden 2000). If polyploidization is strongly correlated with self-compatibility then neopolyploid species should generally have very small flowers as well. Anecdotal evidence thus far indicates that polyploid species are found among lineages spanning a large range of flower sizes, from small wind-pollinated grasses (of which, the majority are polyploid) (Hilu 2004), to the large, insect-pollinated inflorescences of *Chamerion angustifolium* (Husband and Sabara 2004; Fig. 1). This indicates that the relationship between pollination mechanism, self-compatibility, and polyploidy is not amenable to interpretation without information regarding its phylogenetic context. We intend this review to (1) point out some pollination-related macroecological factors that may be confounded with previously-documented correlates of polyploidy; (2) compile existing data regarding floral display and polyploidy; and, (3) indicate future research that would help to elucidate which pollination-related factors facilitate polyploid establishment.

## MACROECOLOGY OF POLYPLOIDY, MATING SYSTEMS, AND POLLINATION

### Mating system correlates

Mating system, like polyploidy, is not uniformly distributed with regard to latitude, altitude, and insularity (Richards 1997). The often-reported correlation between self-compatibility and polyploidy may actually be the result of underlying association between mating system and geography and/or habitat type. Polyploidy has been associated with greater incidence at higher latitudes (Love and Love 1943; Haskell 1952) and altitudes (Johnson and Packer 1965; Petit and Thompson 1999; Brochmann *et al.* 2004; Guggisberg *et al.* 2006), as well as in island floras, including that of New Zealand (Hair 1966), Norfolk Island (De Lange and Murray 2003), and Hawaii (Carr 1978). Self-compatible species are expected to be better able to colonize islands (Baker 1959) while tropical floras are thought to exhibit higher degrees of self-incompatibility (Bawa 1990). Self-compatibility is assumed to be important at high altitudes (but see Smith and Young 1987) because of harsh conditions and short growing seasons, and some degree of self-compatibility has been demonstrated at many high latitudes (e.g., tundra plants; Molau 1993). These patterns are consistent with the idea that polyploidy is highest where self-compatibility is highest. It is currently uncertain whether the general geographic pattern of polyploidy mirrors that of self-compatibility due to a direct association between polyploidy and self-compatibility or because these life history traits are independently favored in common habitats.

### Pollination syndrome

The pollination ecology of most polyploid species is scarcely known, but tentative predictions can be made based on the type of pollinator communities that are found in areas with high occurrence of polyploidy. Island habitats differ in



Fig. 1 Diploid (left) and tetraploid (right) *Chamerion angustifolium*. Photo courtesy of Brian Husband.

their suites of pollinators, and are described variously as rich in small bees (New Zealand; Newstrom and Robertson 2005), nectarivorous birds (Macronesia; Valido *et al.* 2004), and dipterans (Juan Fernandez islands; Bernadello *et al.* 2001). In general, however, island flora are thought to have small, simple flowers and more generalist pollinators (Olesen *et al.* 2002; Abe 2006). Arctic and alpine regions show a dominance in flies as pollinators (Yumoto 1986; Elberling and Olesen 1999) and fly-pollinated species are also more often self-compatible (Yumoto 1986). Conversely, moist tropical rainforests, which are thought to have relatively low frequencies of polyploidy (Love and Love 1943; Morawetz 1986), are thought to also have a high incidence of pollinator specialization (Olesen and Jordano 2002). This information suggests that the context in which polyploidization is thought to occur is most frequently upon a background of self-pollination (or at least self-pollen deposition) via generalist pollinators. Wind pollination also increases with altitude and latitude, and is relatively uncommon in the tropics (Regal 1982), suggesting that anemophily may also provide a context for polyploidization.

Based on the macroecology of polyploidy, mating system, and pollination syndromes, we expect that either insect pollination by generalist small bees and/or flies, or wind pollination, will predominate for the majority of polyploid species. We can further speculate on the expected floral phenotypes of entomophilous polyploids if we consider the typical morphological traits of plant species with generalist pollinators and high selfing rates. Plant species that are typically visited by generalist pollinators are thought to be radially symmetric (e.g., Sargent 2004). Studies within specific groups, such as *Euphrasia* (French *et al.* 2005) and global cross-species comparison (Snell and Aarssen 2005) indicate that selfing species often have smaller flowers. Mechanistically, this correlation between small flowers and selfing may arise due to differences in development, with large-flowered species experiencing delayed anther-stigma contact compared to small-flowered sister taxa (Armbruster *et al.* 2002). Finally, some preliminary evidence indicates that selfing species have more flowers per inflorescence (Sato and Yahara 1999), than do relatively more outcrossing species.

## FLORAL DISPLAY CORRELATES OF POLYPLOIDY – THEORETICAL CONSIDERATIONS

The interaction between selfing rates, inbreeding depression and autotetraploid establishment has been recently explored in more detail with two models (Rausch and Morgan 2005; Yamauchi 2006). Rauch and Morgan (2005) demonstrated that higher selfing rates and lower inbreeding depression in autotetraploids are expected to facilitate establishment of autotetraploid populations. An important outcome of these models is the identification of pollen limitation (Rausch and Morgan 2006) and pollen discounting (Yamauchi 2006) as important factors in autotetraploid establishment. In order to better understand the implications of these models on geographic and phylogenetic patterns of polyploidy we must consider the relationship between pollen limitation and flower size (Knight *et al.* 2005) as well as the ecological determinants of pollen limitation. We must also determine whether changes in floral morphologies with polyploidization tend to result in higher self-fertilization (e.g., reduced flower size and pollinator reward) (Schoen *et al.* 1996). In Yamauchi's model (2006), increases in pollen discounting make autotetraploid establishment more difficult. Pollen discounting is thought to increase when species have large inflorescences (Harder *et al.* 2004) and references therein) and a large proportion of self pollen is delivered to flowers on the same plant through within-plant pollinator movement (geitonogamy). Thus, if the Yamauchi model has widespread applicability, polyploidy should be rare amongst species with large (many-flowered) inflorescences.

Polyploids are expected to differ in flower size from their diploid progenitors (Stebbins 1971), yet whether they display an overall bias towards larger or smaller flowers is not clear. Flower size is expected to diminish in polyploids relative to diploid relatives due to the previously discussed correlations between mating system, geography, and ploidy. In contrast, polyploids can have larger flowers than their diploid progenitors due to the "gigas effect", which is an increase in polyploid cell size that often results in increased organ size throughout the plant (Stebbins 1971). Although these increases in cell size and growth appear to quickly decrease within a few generations (Otto and Whitton 2000), their rapid but short-lived manifestation may still be of great importance during the initial establishment phase when polyploid cytotypes are rare. Larger floral displays of polyploids may encourage visitation by pollinators (Taylor and Smith 1979; Totland 2001), or even change the relative frequency by which specialist versus generalist pollinators visit. However, selection for larger floral displays may only be important when pollinators are choosy, scarce, or unpredictable (Vamosi and Otto 2002; Harder and Johnson 2005), increasing the likelihood of floral display influencing polyploid establishment in alpine and tundra conditions.

The combination of theoretical expectations from models including inbreeding depression and our understanding of pollination biology of polyploids is complex. We can predict small inflorescences (to reduce pollen discounting) and small flowers (to increase selfing and so reduce the frequency of mating with diploid progenitors), but incidental increases in flower size with doubling of the chromosome content can increase pollinator attraction as well as herkogamy, thereby decreasing the selfing rate (Webb and Lloyd 1986; Barrett and Eckert 1990). If these morphological and mating system changes promote outcrossing, then it would seemingly amplify the effects of minority cytotype disadvantage when polyploid cytotypes are rare, and thereby reduce the likelihood of tetraploid establishment. This could be counteracted if assortative mating takes place, either via pollinator constancy to cytotypes that demonstrate variation in floral rewards, or via deposition of pollen on different locations of a pollinator's body due to floral-size differences between cytotypes (the latter mechanism perhaps being more likely in bilateral flowers). While polyploidization can create initial differences in floral morphology amenable to assortative mating, subsequent evolutionary reinforcement could be expected to promote the evolution of further reproductive isolation due to the fitness cost of producing mixed-ploidy offspring (Whitton 2004; Nuismer and Cunningham 2005). Such isolating mechanisms need not be qualitatively the same as those that are directly tied to polyploidization, and the extra genomic content of a polyploid may facilitate relatively rapid evolution of novel floral phenotypes. For example, over longer time periods, the additional genomic content within polyploids may facilitate the evolution of novel structures such as nectar spurs and additional petals (Levin 1983). Below, we review the evidence of the correlates of polyploidy with floral display traits of plants and reflect further on how these correlates arise.

## POLYPLOIDY AND POLLINATION– EMPIRICAL PATTERNS

There is surprisingly little direct empirical evidence on the relationship between floral display and pollinator preferences in mixed cytotype populations despite the recognition that the extent of pollen transfer within and between newly formed polyploids, triploids, and diploids represents an important first step (or barrier) in tetraploid establishment (Thompson and Lumaret 1992; Thompson *et al.* 1997, 2004). However, some inferences can be made by indirect comparisons of floral morphologies and pollinator syndromes. Larger polyploid flowers are evident in *Chamerion angustifolium* (Husband and Schemske 2000; Kennedy *et al.* 2006). Yet there are numerous cases (e.g., *Claytonia parvi-*

flora (Miller and Chambers 1993); *Tarasa* (Tate and Simpson 2004), and *Amsinckia gloriosa* (Johnston and Schoen 1996)) in which polyploid flowers are smaller and have higher selfing rates than diploid progenitors. We review (1) the studies that have directly examined pollinator dynamics between polyploid and diploid pollinator dynamics; 2) the studies that have examined floral display metrics between polyploid and diploid individuals of the same or closely related species. We divided autopolyploids and allopolyploids because widely disparate mechanisms are required to generate polyploids in each. Because there may be a research/publication bias, in that cases where polyploids and diploids differ in floral features are more likely to be examined, we have also gathered floral display metrics for species within Ranunculaceae, and the genera of Rosaceae and *Plantago*, where ploidy information was available to investigate whether there are predictable cross-taxa correlates between polyploidy and flower size, the number of flowers per inflorescence, and pollination syndrome attributes.

### Polyploidy and pollinator choice

What little evidence is available seems to indicate that pollinators with a high degree of flower constancy may facilitate polyploid establishment. A high degree of flower constancy increases the chance that newly formed polyploid genotypes will receive pollen from plants of like ploidy and avoid the strong fitness costs associated with producing unfit hybrids (Levin 1975). Kennedy *et al.* (2006) found that within mixed-ploidy populations of *C. angustifolium*, 73% of all pollen came from within-ploidy pollinations, mirroring pollinator foraging behaviour. Tetraploid establishment is likely facilitated in mixed-ploidy populations of *C. angustifolium* because pollinators also exhibited higher constancy on tetraploids and visited them disproportionately, likely because tetraploids have significantly larger and more open flowers per inflorescence than diploids (Husband and Schemske 2000; Kennedy *et al.* 2006). Similarly, floral visitors strongly discriminated between diploid and tetraploid *Heuchera grossularifolia*, which also exhibits morphological differences between cytotypes (Segraves and Thompson 1999). Although visitation rate did not differ between the cytotypes in *H. grossularifolia*, diploids were visited preferentially by sweat bees and bumble bee workers, while tetraploids were preferentially visited by beeflies (*Bombyllius major*), moths (*Greya politella*) and bumble bee queens (*Bombus* spp.) (Segraves and Thompson 1999).

These two species are apparently the only ones that have been examined to test the idea that pollinators might

discriminate between cytotypes. More studies are clearly needed to address the long-standing hypothesis that polyploid establishment should be favored when there is high flower constancy of pollinators. If flower constancy is important for polyploid establishment, we would predict the incidence of polyploidy should be higher in plant species pollinated by social bees or birds compared to those that are fly or wind pollinated. Yet, this prediction is opposite to that expected from the higher levels of polyploidy in ecosystems dominated by generalist pollinators (i.e. high altitudes or latitudes). To our knowledge no comparative test of these predictions has been conducted.

### Comparison of floral display between polyploid and diploid individuals

We compiled the evidence for increases in floral display with increases in ploidy level for autopolyploids (Table 1). We performed a literature search in both the Web of Science and Google Scholar for combinations of the key words polyploid\* and flower (or floral) morph\* or size. We also worked backward through all references identified to locate additional relevant studies. This resulted in 18 species for which the size and/or numbers of flowers was compared between diploids and autopolyploids. We found that polyploid individuals had larger flowers than their diploid counterparts more often than expected by chance (14 of 17 species;  $P = 0.01$ ; sign test). Flower number was reported less frequently, and was larger for polyploids in just 2 of 5 studies (Table 1).

This literature search also identified 13 studies that compared flower size or number between a polyploid species (or group of polyploid species) and either closely related species or species known or believed to be the progenitors of an allopolyploid. In this data set, which compares species that have diverged over a longer evolutionary time frame than those in the autopolyploid data set, we find that polyploids had larger flowers than diploid counterparts in just 6 of 13 cases ( $P > 0.05$ ; sign test), and in only one of the three studies examining flower number did polyploid individuals have more (Table 2).

These results highlight two issues. First, flower size may not be universally larger in polyploids relative to diploids, despite the assumption that this is a common outcome due to the gigas effect. Autopolyploids do tend to have larger flowers than diploids within the same species, and this is the case in the two species that are well-studied in terms of their pollination biology (*C. angustifolium* and *H. grossularifolia*). Flower size differences could assist polyploid establishment in this instance, as discussed previously. Secondly, it is unclear how much publication bias

**Table 1** Within-species comparisons of flower display between polyploid and diploid species for autopolyploids.

Species	Flower size	Larger? <sup>1</sup>	Flower number	Larger?	Reference(s)
<i>Anemone palmata</i>	Tepal number, length	P			Medail <i>et al.</i> 2002
<i>Alyssum maritimum</i>	Petal length	P			Bali and Tandon 1959
<i>Antirrhinum majus</i>	Flower size	P			Emsweller and Ruttle 1941
<i>Arrhenatherum elatius</i>	Panicle length	P			Petit <i>et al.</i> 1997
<i>Asphodelus fistulosus</i>	Tepal length	D			Ruiz Rejon <i>et al.</i> 1990
<i>Chamerion angustifolium</i>	Flower width	P	# Open flowers	P	Husband and Schemske 2000; Kennedy <i>et al.</i> 2006
<i>Dactylis glomerata</i>	Panicle length	P			Lumaret <i>et al.</i> 1987
<i>Deschampsia cespitosa</i>	Glume size	P			Rothera and Davy 1986
<i>Heuchera grossularifolia</i>	Petal length,width	P	# Open flowers	D	Segraves and Thompson 1999
<i>Hibiscus syriacus cultivars</i>	Corolla diameter	P			van Huylenbroeck <i>et al.</i> 2000
<i>Lotus alpinus</i>	Petal size	P	Flowers per umbel	P	Gauthier <i>et al.</i> 1998
<i>Lilium formosium</i>	Flower size	P			Emsweller and Ruttle 1941
<i>Lycium californicum</i>	Flower length	P			Yeung <i>et al.</i> 2005; J. Kohn pers comm
<i>Phlox drummondii</i>	Inflorescence diameter	P	Flower number	D	Garbutt and Bazzaz 1983
<i>Ranunculus adoneus</i>	Floral morphology	I			Baack 2005
<i>Sedum pulchellum</i>			Flowers per inflorescence	D	Smith 1946
<i>Tradescantia spp.</i>	Floral morphology	I			Anderson and Sax 1936
<i>Zea mays</i>	Flower size	P			Randolph 1935

<sup>1</sup>P = polyploidy species is larger; D = diploid species is larger; I = polyploids and diploids are indistinguishable, or polyploid is intermediate

**Table 2** Among-species comparisons of flower display between polyploid and diploid species for allopolyploids.

Polyploid species	Diploid Species	Flower size	Larger? <sup>1</sup>	Flower number	Larger?	Reference(s)
<i>Allium cepa</i> x <i>fistulosum</i>	<i>Allium cepa</i> , <i>A. fistulosum</i>	Flower size	P			Levan 1941
<i>Amsinckia gloriosa</i>	<i>Amsinckia douglasiana</i>	Floral length, width	D			Johnston and Schoen 1996
<i>Anthericum liliago</i>	<i>Anthericum ramosum</i>	Flower diameter	P	Flower number	D	Rosquist and Prentice 2001
<i>Claytonia parviflora utahensis</i>	<i>Claytonia parviflora grandiflora</i>	Flower size	D			Miller and Chambers 1993
<i>Collinsia parviflora</i>	<i>Collinsia parviflora</i> , <i>C. grandiflora</i>	Flower size	I			Tunbridge and Elle unpublished
<i>Digitalis mertonensis</i>	<i>D. purpurea</i> , <i>D. ambigua</i>	Flower size	P			Buxton and Darlington 1931
<i>Draba</i> spp.	<i>Draba</i> spp.	Petal area	P			Brochmann 1993
<i>Euphrasia minima</i>	<i>Euphrasia christii</i> , <i>E. hirtella</i>	Corolla length	I			Liebst and Schneller 2005
<i>Platanthera huronensis</i>	<i>Platanthera aquilonis</i> , <i>P. dilatata</i>	"floral features"	I			Wallace 2004
<i>Senecio cambrensis</i>	<i>Senecio squalidus</i> , <i>S. vulgaris</i>	Capitulum length	P			Abbott and Lowe 2004
<i>Stellaria longipes</i>	<i>Stellaria longifolia</i>	Flower diameter	P	Flowers per ramet	D	Macdonald and Chinnappa 1988
<i>Tarasa</i> spp.	<i>Tarasa</i> spp.	Petal length	D			Tate and Simpson 2004
<i>Tragopogon miris</i> , <i>T. miscellus</i>	<i>Tragopogon dubius</i> , <i>T. porrifolius</i> , <i>T. pratensis</i>	Not examined		Flowers per head	P	Ownbey 1950
<i>Vaccinium uliginosum</i>	<i>Vaccinium myrtillus</i> , <i>V. vitis-idaea</i>	Corolla diameter	D			Jacquemart and Thompson 1996

<sup>1</sup>P = polyploidy species is larger; D = diploid species is larger; I = polyploids and diploids are indistinguishable, or polyploid is intermediate.

influences this result; in some cases the absence of morphological differences from papers with a different focus (e.g. *Ranunculus adoneus*, Baack 2005) and in one case not included in **Table 1** we learned of a lack of morphological difference by inquiring of the author (for *Hieracium echinoides*, T. Peckert pers. comm.).

The lower incidence of larger flowers in allopolyploids relative to autopolyploids may be due to the differing genetic mechanisms involved in hybridization versus genomic doubling. It has been argued that selfing especially facilitates polyploidization in allopolyploids (Grant 1971), attributable to there being a high frequency of spontaneous tetraploids produced by selfed hybrids (Ramsey and Schemske 1998). This is thought to be responsible for the pattern of self-fertilizing polyploids being most commonly of allopolyploid origin (Stebbins 1957). Thus, pollinator dynamics may be relatively unimportant in allopolyploid species and the larger flowers observed in (relatively more outcrossing) autopolyploids may reflect selection for increased pollination. Alternatively, recent molecular work in neopolyploid species indicates that the rate of gene silencing between duplicated allopolyploid and autopolyploid genomes may differ substantially (Adams and Wendel 2005) and this may play a role in whether the gigas effect is observed. Clearly, further research comparing morphology of polyploids with their progenitors is needed to address whether our long-standing assumption about relative flower sizes is true. Too few studies are published at this time for strong conclusions to be made, which is why we chose to improve the number of species within our comparison by compiling data for cross-taxa comparisons.

### Cross-taxa comparisons of Rosaceae and Ranunculaceae

This review suggests that autopolyploid species and genera should have larger inflorescences than diploid species and genera, though the case is less clear for allopolyploids. We delve further into the floral traits (flower size, floral syndrome, flower color) of polyploids versus diploids within Ranunculaceae and Rosaceae.

We obtained ploidy information for Ranunculaceae species included in Mable (2004) from Barbara Mable, and also used the proportion of polyploid species per genera of Rosaceae from Vamosi and Dickinson (2006). For the species and genera within these datasets we found coarse estimates of mean flower diameter (or mean flower depth in the case of zygomorphic flowers) and flowers per inflorescence (coded as solitary vs. not solitary) in species descriptions. The main references for these data include (Kalkman 2004; Tamura 2004), and the E-flora database ([www.efloras.org](http://www.efloras.org)). For Ranunculaceae, we also coded flower color, and flower symmetry traits, as these are expected to influence pollinator choices. Too little variation occurs in Rosaceae to analyze these traits (most Rosaceous species have actinomorphic, white/pink flowers).

We find that these coarse floral display metrics reveal important correlations between floral display and polyploidy. In Ranunculaceae, polyploidy was surprisingly equally proportioned within species in terms of symmetry and flower color (**Table 3**). However, polyploid species had, on average, smaller flowers than diploid species and more often displayed multi-flowered inflorescences. In

**Table 3** Summary of floral display comparisons between species in Ranunculaceae and genera of Rosaceae.

Trait	Ranunculaceae		Rosaceae	
	N	Direction of correlation with polyploidy (P-value)	N	Direction of correlation with polyploidy (P-value)
Flower size (mm)	89	- (0.013) <sup>1</sup>	71	Ns (0.171) <sup>2</sup>
More than one flower per inflorescence (vs. solitary flowers)	117	+ (0.026)	80	+ (0.010)
Symmetry (actinomorphic vs. zygomorphic)	120	Ns (0.589)	N/A	Not done
Color (blue/red/purple vs. white/green/cream/yellow)	108	Ns (0.186)	N/A	Not done

<sup>1</sup> P-values from contingency tests (or t-tests in the case of flower size) between species that were 1-diploid; 2-polyploid; or 3-mixed. Ns = not significant.

<sup>2</sup> P-values from t-tests (for solitary flowers or not) or correlation tests (flower size), comparing arc-sin proportions of polyploid species per genus in Rosaceae. Flower size was ln-transformed mean (in mm) of values obtained for the species or genus. Ns = not significant.

Rosaceae, there is no significant correlation between proportion of polyploidy and mean flower size (Table 3). However, there is strong pattern for genera with solitary flowers to have a much lower incidence of polyploid than genera with >1 flowers/inflorescence ( $F_{1,78} = 6.99$ ;  $P = 0.010$ ). Because of the strong flower size-number trade-off that is observed in many species (Cohen and Dukas 1990; Harder and Barrett 1995; Worley *et al.* 2000), it is perhaps not surprising that a cross-taxa comparison does not reveal flower size to be larger for genera with high levels of polyploidy.

### Cross-taxa comparisons in the wind-pollinated genus, *Plantago*

Because anemophily (aerial pollination) is known to be important in geographic areas where polyploidy is common, we were interested in examining morphological traits in wind-pollinated species that had both high rates of polyploidy and variation in mating system (cleistogamy, or obligate selfing, and chasmogamy, capable of outcrossing). Wind-pollinated species generally have small pollen grains capable of being transported long distances (Ackerman 2000) and floral parts that modify airflow around reproductive structures to maximize pollen capture. Evidence for the adaptive value of pollen grain size comes from a study of *Plantago* demonstrating that pollen grains that arrive on stigmas are smaller than those produced by the species as a whole (Primack 1978) indicating strong selection pressure for this trait. If the gigas effect is a widespread phenomenon, anemophilous polyploids should display larger pollen grain size and larger corolla size unless these traits are under strong selective pressure, either for pollen transport (grain size) or pollen capture (corolla size).

We compiled data on the genus *Plantago*, for which information was available on mating system and pollen size (Bassett and Crompton 1968) as well as chromosome numbers (Bassett and Crompton 1968; Rahn 1996). For the purpose of this review, we define polyploidy in *Plantago* as any  $2n$  chromosome count greater than 12 (Stebbins 1971). For the *Plantago* species examined, polyploidy is more common than the original diploid state (Table 4) while the number of cleistogamous species is roughly equal to the number of chasmogamous species.

Polyploidy was not significantly associated with cleistogamy or chasmogamy ( $\chi^2 = 0.2015$ ,  $P > 0.6535$ ). Pollen grain size is non-normally distributed and is larger in polyploids than diploids (Wilcoxon test,  $W = 158.5$ ,  $P < 0.01$ ). Polyploids also had larger corollas than diploids (t-test,  $t = 3.9$ ,  $df = 13.115$ ,  $P < 0.01$ ). Pollen sizes were not significantly different between cleistogamous and chasmogamous species. Cleistogamous species have more variable pollen grain sizes than chasmogamous species although there is no significant difference in size. Cleistogamous polyploid pollen grains are significantly larger than cleistogamous diploids (Wilcoxon test,  $W = 33$ ,  $P < 0.01$ ). This pattern is also seen in corolla size (t-test,  $t = 9.8445$ ,  $df = 8$ ,  $P < 0.001$ ).

Chasmogamous species have smaller pollen grain sizes and smaller corolla sizes regardless of chromosome complement. These results support the hypothesis that strong selection pressures on chasmogamous species to maximize pollen transport and capture operate to reduce pollen size in these species. The presence of a gigas effect would then only be seen in cleistogamous species where we do see differences in both corolla size and pollen grain size between polyploids and diploids since the variation as a result of polyploidy can be maintained without any direct cost to reproductive success.

Chasmogamous neopolyploids may then be at an initial selective disadvantage because gigas effects would appear to limit pollen capture (changes in corolla size) and pollen dispersal (changes in pollen size). These effects may be ameliorated through rapid selection either for smaller pollen grain and corolla sizes or by transitioning to a cleistogamous mating system. Determining how many independent evolutionary transitions to polyploidy in chasmogamous and cleistogamous lineages would be particularly instrumental in revealing whether gigas effects impose any level of constraint on the evolution of polyploidy in chasmogamous lineages, but this must await phylogenetic analysis.

Polyploidy has effects on both entomophilous and anemophilous pollination syndromes. A large body of information exists for plants with abiotic pollination schemes that would shed more light on the interactions between mating systems and polyploidy.

### DISCUSSION AND FUTURE DIRECTIONS

Geographical and temporal variation in pollinators is recognized as a complicating factor in the evolution of floral display (Sahley 1996; Buide 2006) but this relationship has received little attention in its effects of polyploid origin and maintenance. In any study of polyploid evolution, a basic problem is disentangling the initial effects of polyploid formation from the divergence occurring subsequent to polyploid formation (Stebbins 1971, 1980), and this issue has been considered in recent reviews (Ramsey and Schemske 1998; Wendel 2000; Ramsey and Schemske 2002; Osborn 2004). Because our study was performed at both the within-species and between-species levels, it gives some insight into the processes that might result in the patterns we see. Because within-species comparisons indicate that polyploid individuals most often have larger flowers than their diploid counterparts, polyploidization appears to most often result in larger flowers. However, theoretical predictions suggesting that polyploidization should occur most often in species with (many) small flowers also appear to be true. Thus, species where only polyploid cytotypes are known (or species where both polyploid and diploid races are known) have smaller flowers than purely diploid species or genera because of flower number/size tradeoff and we find correlations between small flowers and polyploidy even though polyploidization may increase flower size.

To our knowledge this paper presents the first report that polyploid species typically have more than one flower per inflorescence. This result was found in both Rosaceae and Ranunculaceae indicating that this may be a general observation and not one restricted to a single family. The few studies that have measured self-pollination within and among flowers found that geitonogamy contributed over 40% of the self-pollination within inflorescences (Leclerc-Potvin and Ritland 1994; Schoen *et al.* 1996; Eckert 2000; Karron *et al.* 2004). Interestingly, our findings of increased flower number provides another avenue leading to a correlation between polyploidy and increased selfing because the incidence of geitonogamy generally increases with display size (Harder and Barrett 1995; Brunet and Eckert 1998; Rademaker *et al.* 1999; Karron *et al.* 2004), as pollinators visit more flowers per inflorescence. Geitonogamy may thus provide a mechanism for increasing rates of polyploidy by providing a level of selfing necessary for the establishment of a polyploidy population within a diploid matrix. Certainly this mechanism ignores the very real possibility of geitonogamy among multiple single flowers on a plant, and we simply wish to point out that the connection between geitonogamy and polyploidy provides fertile ground for future study.

Further study is also required to tease apart the confounding influences that still mar our ability to detect which traits facilitate polyploidy establishment. First, if genomic doubling results in an increase in the number of flowers per inflorescence (Kennedy *et al.* 2006), then we can not infer that polyploids establish more readily in many-flowered lineages. However, we see little evidence that this is a general

**Table 4** Two way table of species properties for *Plantago*.

	Diploid	Polyploid	Total
Chasmogamous	6	11	17
Cleistogamous	3	11	14
<b>Total</b>	<b>9</b>	<b>22</b>	<b>31</b>

consequence of genomic doubling (see **Tables 1, 2**). Second, because polyploidization can disrupt self-incompatibility mechanisms, it is possible that polyploidy establishes within self-incompatible species with solitary flowers and differences in selfing ability and/ or the number of flowers per inflorescence evolves secondarily. It is thought that self-incompatibility mechanisms break down because of several genetic factors, including increased heterozygosity of the alleles that control pollen phenotype or the loss of function of RNases that break down self-pollen, and different mechanisms may be involved in sporophytic versus gametophytic incompatibility (Chawla *et al.* 1997; de Nettancourt 2001). What is not known, however, is whether the breakdown in self-incompatibility (regardless of the causal mechanism) is at all correlated with an increase in flowers per inflorescence. Specifically, comparative phylogenetic analysis at the species level of Ranunculaceae may be revealing of the order of trait evolution.

Within species, it appears that polyploids have larger flowers than their diploid counterparts. Within species, increased flower size has been observed to increase visitation and reproductive success in a number of species (Bell 1985; Connor 1997; Elle and Carney 2003). Our data on *Plantago*, a wind-pollinated genus, indicate that increases in floral size can occur regardless of the functional significance of increased floral size. Although the gigas effect does seem to exist in many polyploid species, it is not a universal feature of all polyploidization events. Our data indicate that associations between polyploidy and larger flowers are only present among autopolyploids and future efforts should concentrate on why this might be the case. An important factor may be that the polyploids and diploids being compared are separated by fewer generations in the autopolyploids for which we have data, as the gigas effect has been seen to disappear within a few generations when there are selection pressures to reduce floral size. Truly, there was surprisingly little information regarding flower size and polyploidy and a careful assessment of the degree of publication bias is required before concrete conclusions can be made. Finally, there is a decided lack of information on how the gigas effect would manifest itself mechanistically. Developmental genetic studies indicate that the duplication of regulatory MADS-box genes plays an important role in floral diversification, yet whether polyploidy is responsible for these duplications is unknown (Kramer *et al.* 1998).

Polyploidy seems to have little association with other floral traits. We necessarily divided Ranunculaceae into coarse groupings based on symmetry and floral color and found little indication that polyploidy has any effect on either trait, and therefore little evidence that polyploid establishment is greatly facilitated when it arises within species employing flower-constant pollinators (bumbebees, birds). Although inflorescence architecture has been posited as important in determining pollinator identity and behavior (Harder *et al.* 2004), and thus could influence whether polyploidy could establish, too little variation in inflorescence type exists in either Rosaceae or Ranunculaceae for us to perform a meaningful test. Therefore, relationships between inflorescence architecture (cyme, raceme, umbel) and polyploidy remains an uncharted avenue of future research.

These newfound correlates between floral display and polyploidy influence the interpretation of traditionally-recognized correlates of polyploidy. Pollen delivery challenges have long been recognized as a potential barrier for tetraploid establishment and this led to hypothesized correlations between self-compatibility, perenniality, and polyploidy (Stebbins 1971). Yet despite the nearly 40 years of conjecture regarding how pollen delivery could change upon polyploidization, we have remarkably few comparative or experimental examinations to base our theories on. The need is readily apparent and we implore more empirical pollination biologists to examine ploidy as a factor in their work.

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