

## SHORT REVIEW

# Genetic constraints on floral evolution: a review and evaluation of patterns

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The characteristics of flowers influence most aspects of angiosperm reproduction, including the agents of pollination and patterns of mating. Thus, a clear view of the forces that mediate floral phenotypic evolution is central to understanding angiosperm diversity. Here, we inform on the capacity for floral phenotype to respond to selection by reviewing published data on heritabilities and genetic correlations for several classes of floral traits (primary sexual, attraction, mating system) in hermaphroditic plants. We find significant heritability for all floral traits but also variation among them, as well as a tendency for heritability to vary with mating system, but not life history. We additionally test predictions stemming from life history theory (eg, negative covariation between male–female traits and flower

size-flower number), and ideas concerning the extent and pattern of genetic integration between flowers and leaves, and between the sexes of dioecious and gynodioecious species. We find mixed evidence for life history tradeoffs. We find strong support for floral integration and its relation with floral morphology (actinomorphy vs zygomorphy) and for a decoupling of floral and vegetative traits, but no evidence that modular integration varies with floral morphology. Lastly, we find mixed evidence for a relationship between the level of sexual dimorphism in attraction traits and the between-sex correlation in gender dimorphic plants.

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## Introduction

In plants, as in any organism, the standing level of genetic variation and covariation is a central determinant of a response to selection, and thus, fundamental to evolution by natural selection (Blows and Hoffmann, 2005). Reviews of empirical work conducted over the last couple of decades have provided a general picture of the strength and shape of selection in the wild (Kingsolver *et al.*, 2001; Geber and Griffen, 2003; Ashman and Morgan, 2004) as well as insight into the levels of genetic variation in functional (Geber and Griffen, 2003), physiological (Arntz and Delph, 2001) and life history characters in wild plants (Mazer and Leubhn, 1999). But as of yet, we have not developed a general understanding of the pattern of genetic constraint underlying the evolution of floral traits, despite the importance of flowers in plant mating and reproduction, as well as their central role in speciation.

While it is well established that flowers are central targets of selection imposed by pollinators (reviewed in Ashman and Morgan, 2004) and other agents (Strauss, 1997) we still do not have a clear understanding of the degree to which floral phenotypes reflect the action of natural selection relative to underlying genetic or developmental constraints (Conner, 2002). Two outstanding questions in floral biology are: (1) Do floral traits

harbor the potential to respond to selection, and if so, which traits or which types of plants have the greatest capacity to respond? and (2) To what degree is floral phenotype constrained by genetic or developmental integration between floral traits, floral and vegetative traits or between sex morphs? Here, we shed light on these general questions by quantitatively assessing published data on heritabilities and genetic correlations for several classes of floral traits. In the next sections, we describe the specific questions we addressed, and the comparisons we performed.

First, we describe the extent and pattern of genetic variation among several categories of floral traits (primary sexual, attraction, and mating system) and among plants with differing mating systems or life histories. An understanding of the variation among traits in their capacity to respond to selection is necessary to make predictions concerning their likely evolutionary trajectory. For instance, whether limited pollination service leads to the evolution of reduced reliance on pollinators (ie, mechanisms of self-pollination) or enhancement of traits that attract pollinators (Ashman and Morgan, 2004), will depend not only on the strength of selection on these traits but also on their ability to respond to selection. Traits may vary in their ability to respond to current selection for a variety of reasons (reviewed in Blows and Hoffmann, 2005). For example, a trait may have low genetic variation relative to other traits because it was subject to strong selection in the past, for example, fitness-related traits such as pollen and ovules (Roff and Mousseau, 1987), or it may have greater sensitivity to environmental variation (plasticity), for example, nectar or female sexual traits (Havens *et al.*,

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1995; Mitchell, 2004). We also sought to determine if genetic variation in floral traits was associated with mating system or life history. Specifically, we determined if genetic variation was lower in self-compatible plants than in self-incompatible ones because the former are on average expected to be more inbred and less genetically variable (Charlesworth and Charlesworth, 1995). We also determined if annuals had lower-genetic variation than perennials because they have shorter generation times (Mazer and Leubhn, 1999) or their population sizes are more variable and thus, likely to experience bottlenecks (Geber and Griffen, 2003).

Second, we drew on life-history and sex allocation theory, as well as ideas about genetic and developmental integration to guide our exploration of genetic covariation between floral traits, between floral and vegetative traits, and between the sex morphs of gender dimorphic species. Specifically, we explored the level of support for resource allocation tradeoffs that are fundamental assumptions of life history and sex allocation theories. We sought to determine whether male and female traits (Ashman, 2003) or flower size and number (Morgan, 1993; Worley and Barrett, 2000) are negatively genetically correlated. We also determined whether male–female correlations varied with mating system because Mazer and Delesalle (1998) argued that mating system dependent-selection could lead to different patterns of correlation. They proposed that gender in self-compatible autogamous taxa may be under stabilizing selection, leading to positive correlation between male–female traits. In contrast, they argued that in self-incompatible taxa, gender may be under diversifying selection, that is, selection for gender specialists, leading to negative male–female correlations. We then explored the extent of overlap in genetic determination of flower and leaf morphology (eg, Kim *et al*, 1999), as it informs on whether floral phenotype may also be shaped by selection acting on vegetative traits (or vice versa, eg, Delph *et al*, 2005). We determined if floral–floral correlations were higher than floral–vegetative correlations because the former are functionally related and may have greater genetic and developmental integration than the latter (Berg, 1960; Conner and Via, 1993; Armbruster *et al*, 1999; Juenger *et al*, 2005). We also determined whether this pattern differed between species with actinomorphic and zygomorphic flowers. It has been suggested that plants with zygomorphic flowers receive more specialized pollination and thus may exhibit strong covariation among functionally interacting floral parts but not between floral and vegetative organs (Berg, 1960; Armbruster *et al*, 1999). In contrast, plants with actinomorphic flowers which receive more generalized pollination may not experience selection for decoupling of floral–vegetative covariation nor strong selection for floral integration, and as a consequence may have lower correlation between floral parts but greater between floral and vegetative ones relative to zygomorphic species (Berg, 1960; Armbruster *et al*, 1999). Lastly, we explored constraint on the evolution of sexual dimorphism in floral phenotype. Sexual dimorphism can evolve if the genetic correlation between homologous traits expressed in the sex morphs is less than one (Lande, 1980; Ashman, 2003). To test this idea broadly, we determined whether the magnitude of the between-sex correlation could predict the level of sexual dimor-

phism in two floral traits (Ashman, 2003) in dioecious and gynodioecious plants. To additionally inform on the capacity for independent evolution, we determined whether male–female correlations are smaller across the sex morphs in dimorphic populations relative to those within hermaphrodites of hermaphroditic populations.

## Methods

### Data source

Our primary data set was compiled from estimates of heritability ( $h^2$ ) and genetic correlation ( $r_g$ ) from 68 studies of hermaphrodite plants published between 1980 and 2005 in *American Journal of Botany*, *Biological Journal of the Linnean Society*, *Bulletin of the Torrey Botanical Club*, *Euphytica*, *Evolution*, *Evolution and Development*, *Functional Ecology*, *Genetics*, *Heredity*, *International Journal of Plant Science*, *Journal of Evolutionary Biology*, *New Phytologist*, *Oikos*, and *The American Naturalist*. While there are limitations to the use of these parameters rather than others, for example, genetic (co)variances or coefficients of variation (Houle, 1992), and concerns about bivariate comparisons for assessing constraints (Blows and Hoffmann, 2005) they are the most widely reported parameters and thus offer the greatest potential for comparison at this time. It should be kept in mind, however, that differences in  $h^2$  could be due to differences in phenotypic variation and/or genetic variation. We considered both broad- and narrow-sense  $h^2$ , since some studies derived estimates based on clones, full-sib or open-pollinated families. The broad-sense  $h^2$  include nonadditive sources of genetic variation and thus are expected to be larger (Falconer, 1989), but may be appropriate to estimate response to selection for largely inbreeding or vegetatively reproducing plants. We tested for differences between broad- and narrow-sense  $h^2$  in our data set. For correlations, we pooled all methods of estimation because sample sizes were low. We also compiled a second data set that included seven dimorphic (dioecious or gynodioecious) species. This data set was used to test hypotheses concerning genetic covariation and sexual dimorphism.

### Data description

In our primary data set, we recorded data on three classes of floral traits: (1) primary sexual based on either male or female organs; (2) attraction measured at the flower or inflorescence levels, as well as reward; and (3) mating system. Male primary sexual traits included all aspects of male allocation including pollen production (size and number), and anther (or stamen) size, shape, or number. Female primary sexual traits included aspects of female allocation such as fruit, seed or ovule production (eg, number, mass) and pistil (or style) size, shape, or number. Both male and female traits were measured mostly at the level of individual flowers. Attraction traits at the flower level were confined to those related to corolla, that is, corolla and petal dimensions (eg, length, width, depth, area, and mass), whereas those at the inflorescence level were confined to aspects of flower number, that is, total and daily flower number. Attraction traits pertaining to reward included all aspects of nectar production (ie, rates, volume, concentration, and sugar

content) and nectary size. Mating system traits included stigma exertion/position, anther exertion/position, anther/ovule ratios, stigma-anther distance, proportion male or female flowers, and indices of autonomous autogamy or self-incompatibility. We also recorded data on vegetative traits ( $r_g$  only) for the subset of studies that reported them. These involved measures of leaf and plant dimension (ie, length, width, area, and perimeter; plant height, rosette diameter, and shape), as well as leaf or stem number, and plant dry biomass.

### Data analysis

We included all estimates of  $h^2$  in the data set even if they were outside theoretical bounds (ie,  $0 < h^2 > 1$ ). We performed the analyses on these raw values, as well as when extremes were truncated to 0 or 1 and when  $h^2$  was arcsine transformed. In all cases the results were qualitatively in agreement, so we only present those based on raw data. To meet the assumptions of ANOVA on  $r_g$  we identified outliers as greater than  $\sim 3$  SD from the mean (generally as  $-1.25 < r_g > 1.25$ ) and removed these prior to analyses. Results were qualitatively similar between analyses prior to and following outlier removal, and we present the analyses on the latter. We explored the variation in genetic parameters on two hierarchical levels: (1) an 'All' level which contains estimates for all traits reported for a particular category of interest; and (2) a 'Population' level which contains one randomly chosen  $h^2$  or  $r_g$  per trait category per population. We acknowledge that the 'All' data set is a liberal treatment of the data and that the degrees of freedom for analysis of this data is inflated because all estimates are not independent. However, it does provide our most complete view of genetic parameter variation and we use it to test hypotheses concerning overall trait variation in  $h^2$  only. The population data set, on the other hand, still suffers from nonindependence, but is more conservative and we use this data set to address the all other hypotheses concerning hermaphrodite species.

We used one-way ANOVA to compare  $h^2$  across trait types, and two-way ANOVAs to determine if  $h^2$  or  $r_g$  differed among trait and species types (eg, mating system, life history, or floral morphology). If data was lacking (less than five estimates per cell) for a given comparison, we did not perform a statistical analysis.

We assessed the evidence for resource allocation trade-offs within primary sexual (male, female) or attraction categories (corolla, inflorescence) separately by comparing  $r_g$  between traits of the same type (eg, female–female) versus  $r_g$  between different types (eg, female–male). As these analyses involved testing nonindependent data for several different hypotheses, we used Bonferroni adjustment of significance values for each analysis.

We determined whether there was a relationship between the level of sexual dimorphism and the between-sex correlation using correlation analysis. We used one value of the between-sex correlation for one attractive trait at each level (flower and inflorescence) per species, when available, and we constructed two different indices of sexual dimorphism: (1) the absolute difference between male (or hermaphrodite) and female trait values relative to their mean value and (2) absolute difference between male (or hermaphrodite) and female trait values relative to the average of the SE (McDaniel, 2005).

### Caveats of our analyses

The results of our analyses must be interpreted with some caution because  $h^2$  and  $r_g$  estimated on multiple traits from the same population of plants are clearly not independent. As a result of this and the fact that many studies do not report the necessary statistics; we did not conduct a formal meta-analysis (Gurevitch and Hedges, 1999). Moreover, there is much debate over whether these genetic parameters can be appropriately subjected to any type of meta-analysis (Markow and Clarke, 1997; Whitlock and Fowler, 1997). As a result of this, some authors have resigned themselves to qualitative comparisons (Kingsolver *et al.*, 2001). However, while our statistical results might need to be viewed with caution, our quantitative approach cannot only inform on the overall patterns but also give us an idea of the magnitude of effects and potential for biologically meaningful differences.

## Results

### Description of data set and studies

The data set contained 604 and 909 estimates of heritability and genetic correlation, respectively, which were derived from 108 populations of 41 species spanning 32 genera and 21 families (Appendix A). Species were primarily self compatible (71%), insect-pollinated (56%) with zygomorphic flowers (63%). Bird- or wind-pollinated species were rare (two species each). Annuals and perennials were equally represented. Most studies (66%) took place under controlled conditions, for example, greenhouses and growth chambers and half of these utilized plant material from full-sib, half-sib, or open-pollinated maternal families. Only 10 studies of nine species (from seven genera and six families) reported vegetative–floral trait correlations for 15 populations. Data on dimorphic species came from seven studies of seven species (Appendix A).

### Pattern of $h^2$ : distribution across traits

For all classes of floral traits,  $h^2$  (Figure 1) was normally distributed with a grand mean of 0.39, which was significantly different from 0 ( $P < 0.001$ ). Mean  $h^2$  was highest for corolla, male and mating system traits, lowest for reward and female traits and intermediate for flower number (Figure 1). There were significant ( $P < 0.0001$ ) differences in  $h^2$  among traits in the 'All' data set even after Bonferroni adjustment, but not the 'Population' data set, although the patterns were the same. While broad sense  $h^2$  were slightly larger, they did not differ from narrow sense  $h^2$  ( $P > 0.10$ ) and thus all were pooled for the majority of subsequent analyses.

### Pattern of $h^2$ : mating system

Sufficient data were available only to compare self-compatible and self-incompatible species with respect to narrow-sense  $h^2$  for male, female and corolla traits. Across all three traits, self-compatible species had lower  $h^2$  than self-incompatible species ( $P < 0.04$ ; Figure 2; Table 1). However, this did not retain significance after Bonferroni correction.

**Pattern of  $h^2$ : life history**

Differences in  $h^2$  between annuals and perennials were always slight and nonsignificant (annuals *vs* perennial pooled across all traits:  $0.40 \pm 0.026$  *vs*  $0.40 \pm 0.025$ ; Table 1).

**Pattern of  $r_g$ : evidence for tradeoffs?**

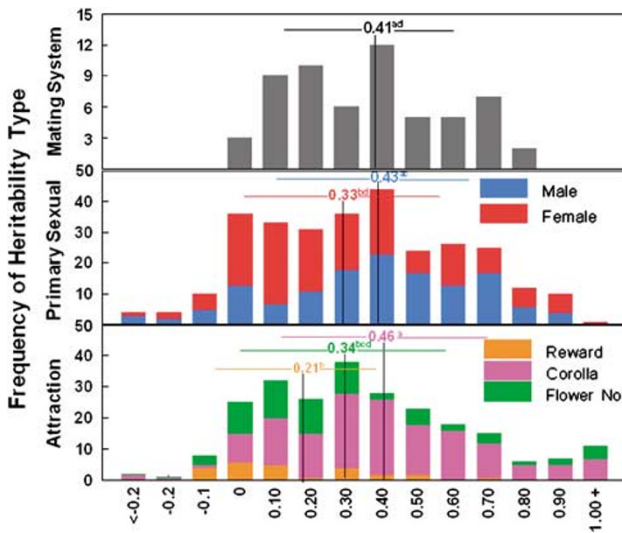
Across traits, we detected a general pattern of significant positive covariation (all  $r_g > 0$ ; significant after Bonferroni correction; Figure 3; Table 1), with one exception. For primary sexual traits there were no significant differences among  $r_g$ , and thus no evidence for a tradeoff between male and female traits within flowers (Figure 3 top; all  $P > 0.1$ ). In contrast, there were differences in correlation for attraction traits that remained significant

after Bonferroni correction (Figure 3 bottom;  $P < 0.0002$ ). Correlations between corolla size traits or between inflorescence traits were high and positive ( $P < 0.001$ ) whereas  $r_g$  across corolla and inflorescence traits was not significantly different from 0 ( $P > 0.30$ ). In fact, when only narrow-sense correlations are considered, the average  $r_g$  across corolla and inflorescence traits is negative ( $-0.03 \pm 0.077$ ), suggesting that the difference in correlation is due to an underlying tradeoff.

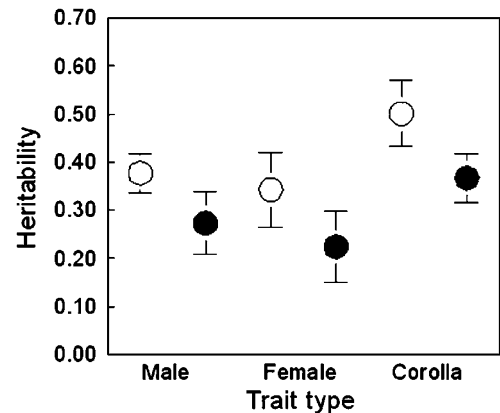
We also tested whether male-female  $r_g$  was lower in self-compatible species than self-incompatible ones, but found no significant difference (SC:  $0.47 \pm 0.016$  *vs* SI:  $0.38 \pm 0.109$ ;  $N = 10$ ;  $P > 0.50$ ).

**Pattern of  $r_g$ : floral *versus* vegetative**

We compared correlations between floral traits (sexual and attraction traits only) to those between floral and vegetative traits and found the average level of  $r_g$  between floral traits ( $0.32 \pm 0.028$ ) was significantly ( $P < 0.008$ ) higher than that between floral and vegetative traits ( $0.15 \pm 0.067$ ). In fact, the correlation between floral and vegetative traits was not significantly different from 0 after Bonferroni correction (Table 1).



**Figure 1** Frequency histograms of  $h^2$  for floral traits by category, that is, mating system (top), primary sexual traits (middle), and attraction (bottom). Mean and SE for each trait type is denoted by a vertical and horizontal bar, respectively. Means that do not share letters are significantly different from each other as determined by a Tukey's test.



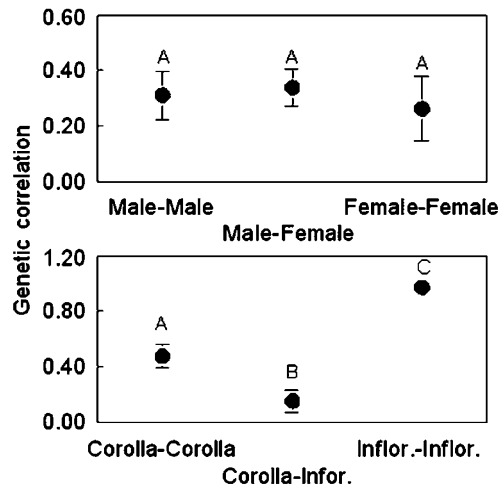
**Figure 2** Mean  $h^2$  ( $\pm$ SE) for male, female and corolla traits for self-incompatible (empty symbols) and self-compatible (filled symbols) plants. Sample sizes are 21-7.

**Table 1** Summary of predictions and supporting evidence

Prediction		Significant supporting evidence?
Hermaphrodite $h^2$	Trait variation	Yes <sup>a</sup>
	Self-compatible < self-incompatible	Yes
	Annual < Perennial	No
$r_g$	Male–female tradeoffs	No
	Flower size and number tradeoffs	Yes*
	Floral–floral > floral–vegetative	Yes*
	Floral–floral: actinomorphic < zygomorphic	Yes*
	Floral–vegetative: actinomorphic > zygomorphic	No
Dimorphic $r_g$	Male–female tradeoff: dimorphic > hermaphrodite	No
	Sexual dimorphism inversely proportional to the between-sex correlation	No

<sup>a</sup>Significant only in the 'All' data set although pattern the same in the 'Population' data set.

A 'Yes' in the supporting evidence column denotes significant pattern. An asterisk denotes results that remained significant after Bonferroni correction.



**Figure 3** Mean  $r_g$  ( $\pm$ SE) for primary sexual traits (top) and attraction traits (bottom). Primary sexual traits included traits associated with male and female investment. Attraction traits include those measured at the level of flowers (eg corolla size) or whole inflorescences (eg, flower number). Sample sizes are 53-36 for sexual, 21-5 for attraction, respectively. Within a data set, means not sharing letters are significantly different as determined by a Tukey's test.

#### Pattern of $r_g$ : floral morphology

The average level of  $r_g$  between floral traits was significantly greater in zygomorphic flowers than actinomorphic flowers, even after Bonferroni adjustment ( $0.51 \pm 0.054$  vs  $0.23 \pm 0.030$ ;  $P < 0.0001$ ; Table 1). The strength of the difference between floral-floral and vegetative-floral correlations did not differ between flower types (trait by morphology interaction:  $P > 0.15$ ), indicating that plants with different floral morphologies do not differ in the level of floral-vegetative integration.

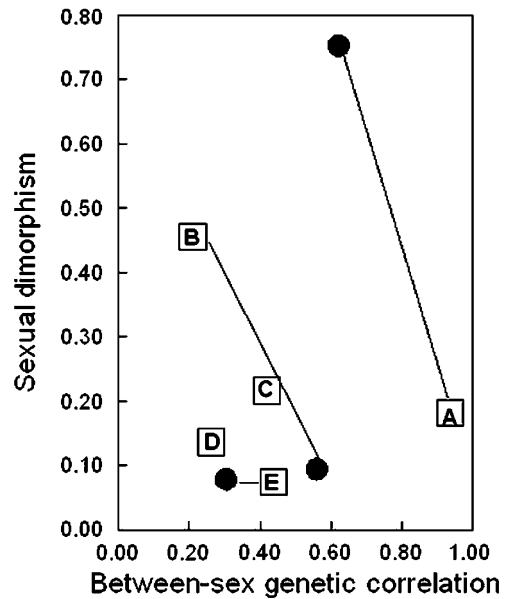
#### Pattern of $r_g$ : gender dimorphism

Male-female correlations across sex morphs in gender dimorphic species were smaller than those within hermaphrodites of hermaphroditic species ( $0.14 \pm 0.265$  vs  $0.34 \pm 0.067$ ) but these differences were based on too small a sample size for gender dimorphics ( $N=3$ ) to warrant a statistical test. Although a clear pattern of higher sexual dimorphism for traits with low between-sex correlation exists for two species (gynodioecious *Fragaria virginiana* and dioecious *Silene latifolia*), this pattern did not exist in gynodioecious *Lobelia siphilitica*, nor across all species combined, regardless of the index of dimorphism used ( $r=0.09, 0.07$ ; both  $P > 0.5$ ; Figure 4).

## Discussion

#### Patterns of $h^2$ for floral traits

**Overall patterns:** The mean estimates of  $h^2$  reviewed here suggest significant genetic variation exists in floral traits and is on par with average heritabilities found in other reviews, for example, 0.43 for physiology, 0.23 for vegetative morphology (Geber and Griffen, 2003). These data also suggest that selection on floral traits may not



**Figure 4** The relationship between the between-sex genetic correlation and the level of sexual dimorphism (absolute difference between the means of the sexes relative to their average standard error) for two attraction traits (corolla size – squares, flower number – circles). Lines connect traits measured in the same species. A – *Fragaria virginiana*, B – *Silene latifolia*, C – *Phacelia lanceolata*, D – *Ecbalium elatrium*, E – *Lobelia siphilitica*.

often be limited by lack of genetic variation. However, because most of the studies reviewed were conducted under controlled conditions and thus, may over estimate  $h^2$  under natural conditions (Conner *et al*, 2003), this conclusion should be viewed with some caution. If one can generalize across species, then these data also suggest that plants harbor an equivalent capacity to respond to selection on corolla or mating system traits. On the other hand, selection response may be expected to be slower with respect to reward and female traits (Figure 1). These patterns are more in line with the idea that high environmental variability, rather than strong past selection, may be the cause of variation in  $h^2$ . Similar conclusions were drawn in a review of plant functional traits (Geber and Griffen, 2003). The only way to truly understand the genesis of these patterns, however, is for more studies to report variance components as well as  $h^2$ . For instance, if both the additive genetic and environmental components of variance are reported then their relative contributions to  $h^2$  for different traits can be assessed.

**Variation associated with mating system and life history:** Even though self-compatible species may have mixed mating systems rather than entirely selfing ones (Goodwillie *et al*, 2005), we found evidence for lower  $h^2$  in self-compatible species compared to self-incompatible ones, although this did not retain statistical significance after correction for multiple tests. Nevertheless, it is suggestive of lower standing levels of genetic variance in more inbred species (Figure 2). This result is in accord with published patterns of lower  $h^2$  for flowering date (Mazer and Leubhn, 1999), and plant functional traits (Geber and Griffen, 2003) in self-compatible relative to incompatible species, and a reduction in the genetic

coefficient of variation for a variety of plant traits with increasing selfing rate (Charlesworth and Charlesworth, 1995). Together these studies begin to lend support to the idea that mating system affects the standing level of genetic variation, and thus the potential for evolutionary response. Future work, however, should endeavor to correlate realized selfing rate with genetic variation of a given trait.

In contrast, we found no evidence for differences in  $h^2$  with life history, a result that is also in accord with the findings of Geber and Griffen (2003) for functional traits, but not with Mazer and Leubhn (1999), who found lower  $h^2$  in annuals than perennials for a wide variety of life history traits. Taken together these findings suggest that differences in  $h^2$  between annuals and perennials depends heavily on how tightly the traits are tied to life history. The lack of difference for floral and functional traits may be due to other features that affect overall variation, such as seed banks buffering against loss of genetic variation in annuals (Nunney, 2002), or the fact that most perennials studied are relatively short-lived and herbaceous, and thus subject to similar fluctuations in population size as annuals. More studies of longer-lived, woody species would be needed to assess this latter hypothesis.

#### Patterns of genetic covariation

**Patterns predicted from life-history and sex allocation theory:** Our results suggest two general patterns with respect to tradeoffs: (1) that  $r_g$  between male and female traits is often positive in hermaphrodite species; (2) that tradeoffs may be more likely across modules rather than within modules.

First, we found positive male–female  $r_g$  across hermaphrodite species (Figure 3). Positive correlation may reflect greater genetic variation in resource acquisition than in allocation (Van Noordwijk and de Jong, 1986), or it could have a selective basis. Mazer and Delesalle (1998) have argued that pollen–ovule  $r_g$  may be under stabilizing selection in autogamously selfing species whereas in outcrossing species it may be under diversifying selection. Although not statistically significant, our data on the variation in male–female  $r_g$  with mating system is consistent with this argument, as is the data reviewed by Ashman (2003). We will need comparative studies that combine estimates of male–female  $r_g$  with estimates of selection on sex allocation or selfing rate to fully test these ideas.

In contrast to the pervasive positive correlation within modules for attraction there was no significant correlation between modules. Specifically, although corolla traits were significantly positively correlated, corolla and inflorescence traits were not (or were negatively) correlated. This may indicate a high level of genetic and developmental integration within flowers (Juenger *et al.*, 2005), negative pleiotropy across flowering modules, for example, size and number (Caruso, 2004), or both. Artificial selection experiments (Conner, 2002) or QTL mapping studies (Juenger *et al.*, 2005) would be powerful ways to address these hypotheses. For instance, if artificial selection can not break up correlations (Worley and Barrett, 2000) or QTL colocalize (Juenger *et al.*, 2005) then pleiotropy, or very tight linkage, is likely.

**Patterns predicted from developmental integration within flowers vs between flowers and vegetative organs:** We found support for developmental integration on two fronts: (1) we found stronger integration of traits within flowers and that this was greater in plants with zygomorphic flowers compared to those with actinomorphic flowers; (2) we found stronger correlation among floral traits than between floral and vegetative traits. However, we did not find support for the prediction that floral–vegetative integration should vary with flower morphology. These results suggest that flowers and leaves, despite having some level of overlap in gene expression (eg, Kim *et al.*, 1999) also maintain distinct levels of developmental integration, or restricted sets of pleiotropic loci. Additionally, while the level of integration is increased in zygomorphic flowers, the across-module variation does not differ from that of plants with actinomorphic flowers. While a potentially interesting conclusion, one must note that the floral–vegetative comparisons are based on relatively few plant species, and thus more data must be collected before a final conclusion is drawn. A critical next step in addressing this hypothesis will be to compare the floral–vegetative  $G$ -matrices for pairs of related species that differ primarily in floral morphological type. In addition, taxa for which changes in flower shape have been tied to the function of one or a few genes can be used to evaluate the effects of these genes on vegetative traits (eg, Costa *et al.*, 2005).

#### Patterns of $r_g$ and sexual dimorphism

Across species we did not find support for the predicted inverse relationship between sexual dimorphism and between-sex genetic correlation. This pattern was, however, apparent in two of the three species for which both attractive traits had been measured. It is interesting to note that these two species are dioecious (*Silene latifolia*) or gynodioecious with high female frequencies (*Fragaria virginiana*) relative to the third species (*Lobelia siphilitica*), which is gynodioecious, but with a very low frequency of females. This may suggest that genetic architecture changes as gender dimorphism evolves. Only when more data on additional species is collected will we be able to confirm this. In addition, studies within species that artificially select for increased or decreased sexual dimorphism will also be useful in assessing the liability of the between-sex correlation. It is also important to note that the between-sex correlation is not the only genetic correlation that influences the response to selection in gender dimorphic species, and correlations within the sex morphs could be responsible for the lack of pattern across species (Ashman, 2005).

#### Conclusions

Our review and analysis of genetic (co)variation in primarily hermaphroditic flowering plants has pinpointed several areas where the response to selection on floral phenotype is likely to be constrained by genetic architecture. First, hermaphroditic flowering plants retain a significant capacity to respond to selection on floral phenotype, but this varies with mating system such that self-compatible species may be less able to respond to similar selection than self-incompatible ones.

Second, while pervasive positive genetic correlations between male–female traits may constrain the evolution of gender specialists in outcrossing species, such correlations could facilitate the response to stabilizing selection in autonomously selfing species. Third, strong levels of genetic integration within flowers of zygomorphic plants but not actinomorphic ones might indicate that evolving zygomorphy limits a species' evolutionary options, at least with respect to floral phenotype. Fourth, evidence that floral and vegetative traits are decoupled in both types of plants suggests that vegetative and floral modules may be relatively free to evolve to separate optima.

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## Appendix A

A summary of plant species used for this review. Studies are listed alphabetically within species. Biological features considered in the analysis are noted for each

species: Life history (A) annual, (P) perennial; Compatibility: (SC) self-compatible, (SI) self-incompatible; Floral morphology: (A) actinomorphic, (Z) zygomorphic, or (U)

undescribed. Characteristics of the studies (number of populations, whether  $h^2$  or  $r_g$  were reported) are also noted in Table A1.

Table A1

Species	Life history	Floral morphology	Mating system	No. pops	$h^2$	$r_g$	Reference
<b>Hermaphroditic Species</b>							
<i>Arabidopsis thaliana</i>	A	A	SC	4	Yes	Yes	Juenger <i>et al</i> (2005), Ungerer <i>et al</i> (2002)
<i>Begonia semiovata</i>	A	Z	SC	1	No	Yes	Agren and Schemske (1995)
<i>Brassica campestris</i>	A	A	SI	1	No	Yes	Dorn and Mitchell-Olds (1991)
<i>Brassica napus</i>	A	A	SC	1	No	Yes	Damgaard and Loeschcke (1994)
<i>Brassica rapa</i>	A	A	SI	2	Yes	No	Sarkissian and Harder (2001)
<i>Campanula rapunculoides</i>	P	A	SC/SI	2	Yes	Yes	Good-Avila and Stephenson (2002), Vogler <i>et al</i> (1999)
<i>Clarkia unguiculata</i>	A	A	SC	1	No	Yes	Mazer and Dawson (2001)
<i>Collinsia heterophylla</i>	A	Z	SC	4	Yes	No	Charlesworth and Mayer (1995)
<i>Dalechampia scandens</i>	P	Z	SC	2	Yes	No	Hansen <i>et al</i> (2003), Pelabon <i>et al</i> (2004)
<i>Danthonia spicata</i>	P	Z	SC	2	Yes	No	Clay (1982)
<i>Dimorphotheca pluvialis</i>	A	Z	SC	1	Yes	No	Hof <i>et al</i> (1999)
<i>Eichornia paniculata</i>	A	U	SC	3	Yes	Yes	Worley and Barrett (2000, 2001)
<i>Gilia achilleifolia</i>	A	A	SC	2	Yes	Yes	Schoen (1982)
<i>Gladiolus grandiflorus</i>	P	Z	U	1	No	Yes	Rameau and Gouyon (1991)
<i>Heterosperma pinnatum</i>	A	Z	SC	2	Yes	Yes	Venable and Burquez (1989, 1990)
<i>Impatiens pallida</i>	A	Z	SC	3	Yes	Yes	Bennington and McGraw (1996), Schoen <i>et al</i> (1994)
<i>Ipomopsis aggregata</i>	P	A	SI	4	Yes	Yes	Campbell (1996, 1997a, b), Campbell <i>et al</i> (1994)
<i>Lythrum salicaria</i>	P	A	SI	3	Yes	Yes	O'Neil (1997), O'Neil and Schmitt (1993)
<i>Mimulus guttatus</i>	P	Z	SC	10	Yes	Yes	Carr and Fenster (1994), Fenster and Carr (1997), Mossop <i>et al</i> (1994), Ritland and Ritland (1996), Robertson <i>et al</i> (1994), van Kleunen and Ritland (2004)
<i>Mimulus guttatus x cupriphilus</i>	P	Z	SC	1	No	Yes	Macnair and Cumbes (1989)
<i>Mimulus guttatus x nasutus</i>	P	Z	SC	1	Yes	Yes	Fishman <i>et al</i> (2002)
<i>Mimulus micranthus</i>	A	Z	SC	2	Yes	Yes	Carr and Fenster (1994)
<i>Nigella degenii</i>	A	A	SC	3	Yes	Yes	Andersson (1997)
<i>Penstemon centranthifolius</i>	P	A	SC	2	Yes	Yes	Mitchell and Shaw (1993), Mitchell <i>et al</i> (1998)
<i>Phlox drummondii</i>	A	A	SI	1	Yes	Yes	Lendavi and Levin (2003)
<i>Plantago lanceolata</i>	P	Z	SI	2	Yes	No	Primack and Antonovics (1981), Tonsor and Goodnight (1997)
<i>Polemonium viscosum</i>	P	A	SI	2	Yes	Yes	Galen (1996), Galen and Cuba (2001)
<i>Primula scotica</i>	P	A	SC	1	No	Yes	Mazer and Hultgard (1993)
<i>Primula sieboldii</i>	P	A	SC	1	No	Yes	Nishihiro <i>et al</i> (2000)
<i>Primula stricta</i>	P	A	SC	1	No	Yes	Mazer and Hultgard (1993)
<i>Puccinellia maritima</i>	P	U	U	1	Yes	Yes	Gray and Scott (1980)
<i>Ranunculus reptans</i>	P	A	SC	2	No	Yes	Prati and Schmid (2000)
<i>Raphanus raphanistrum</i>	A	A	SI	6	Yes	Yes	Conner (1997), Conner and Via (1993), Conner <i>et al</i> (2003), Mazer (1987a, b)
<i>Raphanus sativus</i>	A	A	SI	8	Yes	Yes	Mazer and Schick (1991a, b), Stanton and Young (1994), Young <i>et al</i> (1994)
<i>Scabiosa canescens</i>	P	A	SC	6	Yes	No	Waldmann and Andersson (1998)
<i>Scabiosa columbaria</i>	P	A	SC	6	Yes	No	Waldmann and Andersson (1998)
<i>Scleranthus annuus</i>	A	A	SC	1	Yes	Yes	Svensson and Persson (1994)
<i>Solanum carolinense</i>	P	A	SI	3	Yes	Yes	Elle (1998)
<i>Spergularia marina</i>	A	A	SC	7	Yes	Yes	Delesalle and Mazer (1995), Mazer <i>et al</i> (1999), Mazer <i>et al</i> (2003)
<i>Talinum mengesii</i>	P	A	SC	1	Yes	No	Carter and Murdy (1986)
<i>Turnera ulmifolia</i>	P	A	SC	1	Yes	Yes	Shore and Barrett (1990)
<b>Dimorphic Species</b>							
<i>Ecballium elaterium</i>	P	A	SC	1	Yes	Yes	Costich and Meagher (2001)
<i>Fragaria virginiana</i>	P	A	SC	4	Yes	Yes	Ashman (1999, 2003)
<i>Lobelia siphilitica</i>	P	Z	SC	2	No	Yes	Caruso <i>et al</i> (2003)
<i>Phacelia linearis</i>	A	A	SC	3	Yes	Yes	Eckhart (1993)
<i>Silene latifolia</i>	P	A	SI	1	Yes	Yes	Delph <i>et al</i> (2004)
<i>Thalictrum dioicum</i>	P	A	SI	1	No	Yes	Davis (2001)
<i>Thalictrum pubescens</i>	P	A	SC	1	No	Yes	Davis (2001)



## Appendix References

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