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The Limits on Sexual Dimorphism in Vegetative Traits in a Gynodioecious Plant

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ABSTRACT: Gynodioecious plants exhibit modest sexual dimorphism in vegetative and phenological traits, which stands in stark contrast to pronounced dimorphism in reproductive traits. I evaluate the roles of limited genetic variation, negative genetic covariation (within and between sex morphs), and lack of gender-differential selection in contributing to minimal sexual dimorphism for these traits in *Fragaria virginiana*. Major findings are as follows. First, selection was sometimes differential but rarely divergent between male and female fertility modes. Second, response to selection was constrained by low genetic variation and extensive genetic covariance. In fact, covariance between traits within sex morphs appears to represent a constraint on par with that of covariance between sex morphs. Third, these constraints combine with different modes of gamete transmission to produce very different gender-specific contributions to the mean phenotypes of the next generation. Finally, predicted responses to selection for several traits are concordant with the degree and direction of dimorphism in a closely related dioecious species. In sum, this work suggests that minimal sexual dimorphism in vegetative and phenological traits is due to similar directional selection via male and female fertility combined with the constraints of low genetic variation and extensive genetic covariance both within and between sex morphs.

Keywords: adaptive evolution, antagonistic covariation, dioecy, *Fragaria virginiana*, G matrix, natural selection.

In many plants, sexual dimorphism extends beyond primary sexual traits into life-history and vegetative traits (Dawson and Geber 1999; Delph 1999), but this is not universal. In fact, while gynodioecious species (females and hermaphrodites) often show sexual dimorphism in reproductive traits (e.g., flower size and number) that rivals that seen in dioecious species (Eckhart 1999; Shykoff et al. 2003), the degree of dimorphism in vegetative traits is

often not as pronounced or absent altogether. For example, leaf size has been found to be sexually dimorphic, at least in some sites or under some environments, in all (26 of 26) dioecious species studied (table 1), but it is not dimorphic in the majority (five of six) of gynodioecious species studied (table 1). Leaf, stem, and branch number (i.e., degree of ramification) are also more likely to be dimorphic in dioecious (25 of 26) than in gynodioecious (three of four) species (table 1). Such patterns might suggest that dimorphism in vegetative traits evolves after the evolution of separate genders in response to sex-differential selection (Geber 1999), but few have explored this evolutionary mechanism (but see Kohorn 1994; Bond and Maze 1999). In fact, we currently have little data that can address the question, why are vegetative traits in gynodioecious species not more dimorphic?

Lack of dimorphism could result from absent/variable selection for dimorphism or from genetic constraints limiting a response to divergent selection. It has been hypothesized that life-history and vegetative traits ought to be under divergent selection through male and female fertility (e.g., S_F , $-S_M$) because of differential costs or requirements of these modes of reproduction (Delph 1999; Geber 1999; Case and Ashman 2005). For instance, females may be selected to flower later (or less often), invest less in asexual reproduction, or grow more than males, because more total resources are required to successfully mature fruit than to produce pollen. Alternatively, because allocation to male function incurs greater opportunity costs during flowering (i.e., allocation to pollen “trades off” with allocation to vegetative growth; Eckhart and Chapin 1997), males may be selected to produce fewer leaves and grow less during flowering than females. It is not known, however, whether vegetative dimorphism in dioecious species represents direct responses to the distinct requirements for male and female reproduction (Kohorn 1994; Machon et al. 1995), indirect responses to selection on reproductive characters (Bond and Midgley 1988), or both. For instance, leaf size could be the direct target of selection via female function if larger leaves better support adjacent developing fruits. In contrast, leaf size in males could be selected

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Table 1: Studies of sexual dimorphism in vegetative traits in dioecious, subdioecious, and gynodioecious species

Species	Sexual system	Leaf size	Leaf number	Branch or stem number	Reference
<i>Asparagus officinalis</i>	D		F > M	F < M	Dzhaparidze 1967; Machon et al. 1995
<i>Cannabis sativa</i>	D	F > M	F > M		Dzhaparidze 1967
<i>Diospyros virginiana</i>	D	F > M			Dzhaparidze 1967
<i>Fragaria chiloensis</i>	D	F ≤ M			Hancock and Bringham 1980
<i>Leucadendron</i> spp. (17 species)	D	F > M		F < M (16 of 17 spp.)	Bond and Midgley 1988
<i>Leucadendron xanthoconus</i>	D	F > M		F < M	Bond and Maze 1999
<i>Lindera benzoin</i>	D	F > M	F < M		Cipollini and Whigham 1994
<i>Pistacia mutica</i>	D	F > M	F < M		Dzhaparidze 1967
<i>Populus gradidentata</i>	D				Sakai and Sharik 1988
<i>Populus tremuloides</i>	D				Sakai and Burris 1985
<i>Rhus typhina</i>	D		F < M	F < M	Lovett Doust and Lovett Doust 1988
<i>Rumex acetosa</i>	D		F > M		Korpelainen 1992
<i>Rumex acetosella</i>	D		F < M, F > M	F > M	Lovett Doust et al. 1987
<i>Silene latifolia</i>	D	F > M	F = M	F > M	Meagher 1992; Lyons et al. 1994
<i>Simonsia chinensis</i>	D	F > M			Kohorn 1995
<i>Siparuna grandiflora</i>	D	F < M	F > M	F > M	Nicotra 1999
<i>Cucurbita foetidissima</i>	G	F = H		F = H	Kohn 1989
<i>Daphne laureola</i>	G	F = H			Alonso and Herrera 2001
<i>Lobelia siphilitica</i>	G	F < H			Caruso et al. 2003
<i>Plantago lanceolata</i>	G		F = H	F > H	Olf et al. 1989; Poot 1997
<i>Sidalcea oregana spicata</i>	G	F = H	F < H		T.-L. Ashman, unpublished data
<i>Phacelia linearis</i>	G			F > H	Eckhart and Chapin 1997
<i>Wurmbea biglandulosa</i>	G	F = H			Ramsey and Vaughton 2001
<i>Wurmbea dioica</i>	SD	F = H = M			Ramsey and Vaughton 2002

Note: Direction (e.g., F > M, F < M) of statistically significant sexual dimorphism is noted for each trait and species studied. If sexual dimorphism was nonsignificant in the original study, it is denoted as F = M. D = dioecious; SD = subdioecious; G = gynodioecious; F = female; H = hermaphrodite; M = male.

indirectly as a consequence of selection for increased pollen production (or dispersal) if pollen production is positively correlated with branch number, which is negatively correlated with leaf size (Bond and Midgley 1988). Although studies that quantify selection on vegetative traits in gender-dimorphic species have been repeatedly called for, few have been conducted (but see Kohorn 1994; Bond and Maze 1999), and none have used selection gradient analysis (Lande and Arnold 1983) as a means of describing and assessing variation in selection.

If there is divergent selection on a trait via male and female fertility but sexual dimorphism is not seen, then low genetic variation or the presence of genetic correlations may be limiting response to selection. Vegetative traits have been shown to harbor high levels of genetic variation in hermaphrodite plants, leading Geber and Griffen (2003) to suggest that lack of genetic variation may not be the most common constraint to adaptive evolutionary change in these plants. However, genetic correlations may be particularly important in species with more

than one sexual morph because the response to selection is a function of three forms of genetic covariation: between traits within the sexes, between homologous traits across the sexes, and between nonhomologous traits across the sexes (Morgan and Ashman 2003). These ideas, however, have not been formally explored in a gynodioecious species.

Both positive and negative genetic correlations can constrain adaptive evolution. First, positive genetic correlations can slow evolution if correlated traits are selected in opposite directions (Conner and Via 1992). Second, negative genetic correlations can slow adaptive response if selection favors high values of both traits. In fact, this sort of "antagonistic" correlation can reverse a response to selection if one trait is under positive selection while the other is under negative selection. Size-number trade-offs are a pervasive example of antagonistic covariation, and these have received much attention at the level of reproductive units (e.g., flowers; Worley and Barrett 2000; Caruso 2004; Delph et al. 2004), but they also occur for

vegetative modules (e.g., leaves, branches) and can constrain evolutionary response in these traits as well (Ettersson and Shaw 2001). Third, correlations between traits in the sex morphs can result in correlated responses in one morph that are greater than, less than, or the opposite of what is predicted from selection in that morph alone (Meagher 1999; Morgan and Ashman 2003). Few studies have determined the degree to which genetic correlations alter selection response (but see Campbell 1996; Mitchell et al. 1998; Ettersson and Shaw 2001; Caruso 2004), despite overwhelming evidence that direct selection accounts for only part of total selection, especially on functional traits in plants (Geber and Griffen 2003).

To investigate the microevolutionary dynamics of sexual dimorphism, I conducted a phenotypic selection analysis of several vegetative traits and a phenological trait in a synthetic field population of gynodioecious wild strawberry (*Fragaria virginiana*). I also estimated genetic variation and covariation for these traits under field conditions, providing the most appropriate measures to predict rate of adaptive evolutionary change (Geber and Griffen 2003). Information on selection and genetic (co)variation were combined to predict the multivariate adaptive change across one generation (Lande and Arnold 1983; Morgan and Ashman 2003). I evaluated whether the traits would be expected to evolve in a way that reflected selection, whether genetic architecture would constrain a response to selection, and whether the response was in the direction of greater sexual dimorphism. In doing this, I sought to answer the following questions. First, what is the pattern of phenotypic selection between male and female fertility or between sex morphs (female fertility only)? Second, what is the level of genetic variation and covariation (within and between sex morphs) for vegetative and phenological traits? And third, does genetic architecture limit response to selection? In particular, does genetic covariation facilitate, retard, or reverse response to selection, and do genetic covariances within or between the sex morphs have the most important influence on the response to selection?

Methods

Study Species

Fragaria virginiana (Rosaceae), the Virginian wild strawberry, is a creeping perennial herb that is native to eastern North America (Staudt 1989) and commonly grows in meadows, in old fields, and along road or forest edges. It has a gynodioecious sexual system where females and hermaphrodites coexist. Sex determination is under nuclear control, with male sterility (femaleness) dominant to male fertility (Ahmadi and Bringhurst 1989). Plants reproduce

sexually via seed or vegetatively via stolons (runners). Both inflorescences and runners develop from axillary buds. Females have very high fruit set (~90%), while that of hermaphrodites is low (~20%), even under optimal conditions (Ashman 2003). Wild populations vary in the frequency of females, and females produce the majority of the seed in populations in northwestern Pennsylvania (Ashman 1999).

Plant Material, Cultivation, and Scoring

The intent of this study was to estimate selection, genetic (co)variances, and predicted response to selection for a synthetic field population of *F. virginiana*, so I used plants from a nested breeding design that were grown in a field garden. Here, I briefly summarize cultivation procedures, while full details are available in Ashman (2003). Plant material was originally obtained from three wild populations (PR, HT, W) in Crawford County, Pennsylvania (see Ashman 1999 for details). Within each population, crosses were performed to yield 210 maternal full-sib families nested within 70 paternal half-sib families. In two replicate plantings (2000 and 2001), seedlings from these crosses were planted in a completely randomized design in a field garden adjacent to the Pymatuning Laboratory of Ecology, Crawford County, Pennsylvania. Plants were protected from deer and goose herbivory with netting enclosures; however, no other attempts were made to retard other natural herbivores or recolonization of natural vegetation after planting. Insect pollination was supplemented by hand pollination three times per week. The frequency of females among flowering plants was 50% and 55% in 2000 and 2001, respectively.

For up to eight flowering plants per maternal family (2 progeny/sex morph/year: a total of 1,440 in 2000 and 2,011 in 2001), I recorded leaf size and number at the time of transplanting (hereafter “fall”) and again at the end of flowering (hereafter “spring”). At each measurement time, leaf size was estimated on one fully expanded leaf per plant that was ~1 month old. The width of the central leaflet was measured on the fall leaves, whereas the “best-fit” ellipse (National Institutes of Health Image program; <http://rsb.info.nih.gov/nih-image>) of the area of the central leaflet was measured on the spring leaves. These two methods of estimating leaf size are strongly correlated ($r = 0.998$, $N = 20$, $P < .0001$). I also recorded the number of trichomes on the upper leaf surface of three 154 mm² circular sections from spring leaves (the average of these was used in analyses), the date of first flower (Julian date), and the number of runners produced per plant by the end of flowering. As part of a previous study, total flower and fruit production, pollen per flower, and ovules per flower had been recorded (for details, see Ashman 2003), and

they were used here to estimate female and male fertility (see “Phenotypic Selection”). MANOVA and univariate ANOVAs (with year and sex as fixed effects and population, sire, and dam as nested random effects) were performed to evaluate the sources of trait variation and, in particular, to determine whether there were differences between the sex morphs in vegetative and phenological traits.

Phenotypic Selection

Different forms of selection can operate in each sex morph and through male and female fertilities of hermaphrodites (Morgan and Ashman 2003), so I estimated standardized phenotypic selection gradients via female fertility of females (hereafter, females’ fertility; β'_f), female fertility of hermaphrodites (β'_{Hf}), and male fertility of hermaphrodites (β'_{Hm}) in each year from multivariate regressions of relative fertilities on standardized trait values. Female fertility was estimated as the product of fruit production and ovules per fruit. This is a good estimate of total seed production because seed set per ovule is high under hand pollination (Ashman and Diefenderfer 2001). Male fertility was estimated by assigning each hermaphrodite a portion of the seeds produced within a year based on its relative pollen production. I calculated pollen production as the product of total flower number and pollen per flower. I evaluated the interaction term between year and traits in ANCOVA to determine whether gradients differed between years. Because year-to-year variation was very limited (only two of 21 selection gradients showed significant yearly variation [runner number $\beta'_f = -0.0486$ vs. 0.0844 ; $\beta'_{Hm} = 0.0088$ vs. 0.1974]), I calculated standardized linear selection gradients, using data pooled across years after the effect of year was removed using ANOVA. I present only these estimates and use them to predict response to selection. Because all plants were hand-pollinated and male fertility estimates are based on pollen production alone, traits under selection should be mediated by resource acquisition and allocation (i.e., to meet the differing costs of male and female function) rather than by aspects of pollination.

Genetic (Co)Variation, Heritabilities, and Genetic Correlations

Because the intent of this study was to estimate response to selection for a synthetic population under field conditions rather than to assess population variability in genetic variation, I statistically removed the effects of both planting year and population from the data, using ANOVA, before estimating genetic (co)variances. I estimated variance components and heritabilities from nested ANOVA, following

the methods described in Lynch and Walsh (1998). I estimated additive genetic variance as four times the sire variance component and calculated the narrow-sense heritability as the additive genetic variance divided by the total phenotypic variance. I determined significance of heritabilities by a significant sire effect in the ANOVA and by randomization tests, as in Ashman (2003). In all cases, randomization tests agreed with ANOVA results, so only the ANOVA results are presented. I compared h^2 between sex morphs, using t -tests with bootstrapped standard errors (e.g., Roff 1997; Ashman 2003) followed by Bonferroni adjustments for multiple tests.

I calculated genetic correlations and covariances between traits within each sex morph and within traits between the two sex morphs, using the family-structured progeny data. I performed Pearson product-moment correlations on paternal half-sib family means that were obtained by first averaging same-sexed progeny from each dam and then averaging over all three dams per sire. This method was used to similarly produce estimated covariances within and between the sex morphs, but it may be subject to some bias (Lynch and Walsh 1998). To determine whether correlations between homologous traits in the sex morphs were different from 1, I performed one-tailed t -tests, using bootstrapped standard errors (e.g., Roff 1997). I compared correlations between sex morphs as above.

I tested for overall sex differences in the \mathbf{G} matrix (i.e., deviations from matrix equality $\mathbf{G}_f = \mathbf{G}_H$) by calculating Roff’s T statistic and using randomization to determine significance (Bégin and Roff 2001). I also computed Roff’s $T\%$, which indicates the overall absolute difference between elements in the two matrices as a percentage of the size of the matrix elements.

Estimation of Predicted Response to Selection and Evaluation of Constraints

Total multivariate response to selection ($\Delta\bar{z}_f$, $\Delta\bar{z}_H$) and gender-specific components of total response to selection ($\mathbf{G}_f\beta_f$, $\mathbf{G}_{Hf}\beta_{Hm}$, $\mathbf{G}_{Hf}\beta_f$, and $\mathbf{G}_H\beta_{Hf}$) were estimated from the phenotypic selection gradients pooled across years and the genetic (co)variance matrices according to the formulas developed by Morgan and Ashman (2003), that is,

$$\Delta\bar{z}_f = \frac{1}{2}(\mathbf{G}_f\beta_f + \mathbf{G}_{Hf}\beta_{Hm}), \quad (1)$$

$$\Delta\bar{z}_H = \frac{1}{2}[(\mathbf{G}_{Hf}a\beta_f + \mathbf{G}_Hb\beta_{Hf}) + \mathbf{G}_H\beta_{Hm}]. \quad (2)$$

Here G_F , G_H , and G_{HF} are the genetic (co)variance matrices within females, within hermaphrodites, and between the sex morphs, respectively, whereas β_F , β_{HF} , and β_{Hm} are the selection gradients via females' fertility, female fertility of hermaphrodites, and male fertility of hermaphrodites, respectively. The a and b parameters reflect fitness-weighted sex ratio (Morgan and Ashman 2003). Unstandardized selection gradients were used to determine the gender-specific components of the response to selection. All estimates of selection were used in calculating the responses to selection regardless of significance because these represent the best unbiased point estimates of selection.

To evaluate whether a response to selection is constrained by genetic (co)variation, I calculated standardized gender-specific contributions to response to selection (e.g., $G_{HF}\beta'_F$) by dividing the unstandardized responses by the phenotypic standard deviation for that sex morph and compared these with the standardized selection gradients by t -tests followed by Bonferroni adjustments. If a standardized component of response to selection (e.g., $G_{HF}\beta'_F$) is smaller in absolute value or differs in sign from the standardized selection gradient (e.g., β'_F), then this suggests genetic constraint on response to selection (Conner and Via 1992). To further explore the source of constraint, I partitioned gender-specific contributions to selection response into those due to direct and indirect responses (i.e., due to selection on correlated traits), following Conner and Via (1992). If the indirect response to selection is in the opposite direction of the direct response to selection, then this suggests that genetic correlations are involved in constraining the evolution of the trait (Conner and Via 1992).

I used estimates of gender-specific contributions to response to selection- and fitness-weighted sex ratio parameters in equations (1) and (2) to predict the standardized between-generation change of each trait in females and hermaphrodites. From these values I predicted the consequences for sexual dimorphism.

Results

Standing Sexual Dimorphism and Phenotypic Variation

Although only a small degree of sexual dimorphism was found for vegetative traits and flowering time (table 2), the overall sex effect was significant (MANOVA: $F = 4.14$, $df = 7, 3,277$, $P < .0002$), and univariate ANOVAs indicated that three traits differed significantly between the sexes. Females produced 6% fewer runners and 3% fewer spring leaves and flowered approximately half a day later than hermaphrodites. There was also evidence for significant genetic variation at the level of populations, sires,

Table 2: Phenotypic means (SE) for vegetative and phenological traits of female and hermaphrodite *Fragaria virginiana* grown in a field garden

Trait	Female	Hermaphrodite
Flower date (Julian date)	116.80 (.104)	116.40 (.112)
Fall leaf number	8.76 (.048)	8.93 (.047)
Fall leaf size (mm ²)	32.41 (.094)	32.08 (.091)
Spring leaf number	19.56 (.146)	19.95 (.147)
Spring leaf size (mm ²)	21.17 (.209)	20.96 (.195)
Trichome number	7.90 (.129)	7.79 (.129)
Runner number	8.36 (.100)	8.89 (.104)

Note: Means in boldface are significantly different between the sex morphs, as determined by a significant sex effect in a mixed-model nested ANOVA. $N = 3941$ – 3986 .

and dams, as well as environmentally induced variation (years) for all traits (data not shown).

Phenotypic Selection

Across years, selection was generally weak; however, some gradients were strong, and common patterns emerged (table 3). First, there was significant selection through females' fertility to increase spring leaf number ($\beta'_F = 0.0640$). Second, selection always favored flowering early, and this was strongest through female fertility of hermaphrodites ($\beta'_{HF} = -0.2111$). Third, trichomes were under selection to decrease via all fertility modes, but this did not reach statistical significance. Fourth, fall leaf number and size were always under selection to increase, significantly so via females' fertility and male fertility.

Genetic (Co)Variation, Heritabilities, and Genetic Correlations

Heritabilities ranged from 0.108 to 0.542, and all were statistically different from 0 but not different between the sex morphs (fig. 1). Similar patterns of genetic correlation were seen within the sex morphs (fig. 1), and none differed significantly between the sexes after Bonferroni adjustment for multiple tests. Strong positive correlations existed between runner number and spring leaf number (0.715 and 0.691 for hermaphrodites [H] and females [F], respectively), between fall and spring leaf size (0.396 [H], 0.251 [F]) and number (0.449 [H], 0.397 [F]). Trade-offs were evident for leaf size and number in both seasons and sex morphs (fall: -0.244 [H], -0.142 [F]; spring: -0.137 [H], -0.201 [F]), as well as between leaf traits across seasons (fall leaf number–spring leaf size: -0.149 [H], -0.233 [F]). Significant negative correlations were also present for spring leaf size and trichomes in both sexes (-0.316 [H], -0.353 [F]). Corroborating the between-sex tests above, a randomization test did not detect a difference between

Table 3: Gender-specific standardized selection gradients (β') and gender-specific contributions ($G_F\beta'_F$, $G_{HF}\beta'_F$, $G_{HF}\beta'_{Hm}$, $G_H\beta'_{Hf}$, $G_H\beta'_{Hf}$) to the total standardized predicted multivariate responses to selection ($\Delta\bar{z}_F$, $\Delta\bar{z}_H$)

Trait	Phenotypic selection β'_F (SE)	Standardized gender-specific contributions to predicted responses to selection					
		$G_F\beta'_F$			$G_{HF}\beta'_F$		
		Total	Direct	Indirect	Total	Direct	Indirect
Flower date	-.0098 (.0155)	-.0018	-.0016	-.0002	.0063	-.0038	.0101
Fall leaf number	.0496 (.0168)*	.0385	.0144	.0241	.0262	.0195	.0067
Fall leaf size	.0378 (.0155)*	-.0197^a	.0083	-.0279	-.0060	.0207	-.0267
Spring leaf number	.0640 (.0218)*	.0463	.0104	.0359	.0163	.0109	.0054
Spring leaf size	-.0270 (.0164)**	-.0046	-.0028	-.0018	-.0173	-.0067	-.0107
Trichome number	-.0239 (.0157)	-.0152	-.0127	-.0025	-.0014	-.0133	.0119
Runner number	.0400 (.0212)**	.0373	.0062	.0311	.0064	.0019	.0045
		$G_F\beta'_F$			$G_{HF}\beta'_{Hm}$		
	β'_{Hm} (SE)	Total	Direct	Indirect	Total	Direct	Indirect
Flower date	-.0417 (.0166)*	-.0111	-.0132	.0022	.0028^a	-.0089	.0117
Fall leaf number	.0410 (.0173)*	.0098	.0165	-.0067	.0259	.0139	.0120
Fall leaf size	.0380 (.0167)*	.0091	.0212	-.0121	.0104	.0164	-.0061
Spring leaf number	-.0310 (.0246)	-.0040	-.0047	.0007	.0762	-.0048	.0810
Spring leaf size	.0182 (.0176)	-.0006	.0048	-.0054	.0256	.0057	.0199
Trichome number	-.0161 (.0171)	-.0049	-.0083	.0034	-.0321	-.0050	-.0272
Runner number	.1587 (.0238)*	-.0003^a	.0066	-.0069	.0117^a	.0189	-.0072
		$G_H\beta'_{Hf}$					
	β'_{Hf} (SE)	Total	Direct	Indirect			
Flower date	-.2111 (.0383)*	-.0421^a	-.0495	.0074			
Fall leaf number	.0339 (.0406)	.0305	.0113	.0191			
Fall leaf size	.0024 (.0391)	-.0063	.0010	-.0073			
Spring leaf number	-.0038 (.0573)	.0531	-.0006	.0538			
Spring leaf size	.0580 (.0411)	.0410	.0176	.0234			
Trichome number	-.0588 (.0398)	-.0579	-.0189	-.0390			
Runner number	.1292 (.0553)*	.0131	.0164	-.0033			

Note: Gender-specific contributions are partitioned into the direct response due to selection on the trait and the indirect response via correlated traits. Total responses to selection in boldface are significantly different from the selection gradient by *t*-test.

^a Significantly different from selection gradients after Bonferroni adjustment for multiple tests.

* $P < .05$.

** $.05 < P < .1$.

the G matrices of the sex morphs ($P = 0.67$, $T\% = 133$). Between-sex genetic correlations for homologous traits ranged from 0.070 to 0.610 (table 4). All, except that for runner number, were statistically significantly different from 0 and 1. There were several significant between-sex genetic correlations for nonhomologous traits, and these mirrored patterns seen for within-sex between-trait correlations (table 4).

Predicted Response to Selection

Thirteen gender-specific contributions to predicted selection response differed significantly in their selection gradients (table 3), and five remained significant after table-wide Bonferroni correction. All were significantly smaller

than the selection gradients, indicating that genetic (co)variance was limiting predicted response to selection. Indirect responses opposed direct responses most of the time (12 of 13). Indirect responses are brought about by the combination of positive directional selection on traits within sexes that covary negatively or by the combination of opposing selection on positively correlated traits. In addition, when several traits are under selection, these processes can occur simultaneously. For example, the gender-specific contribution to selection response for fall leaf size in females via their fertility ($G_F\beta'_F$) involves positive directional selection on fall leaf size and fall leaf number ($\beta'_F = 0.0378$ and 0.0496 , respectively), but these are negatively correlated ($r_F = -0.142$). In addition, fall leaf size is positively correlated with spring leaf size ($r_F = 0.251$),

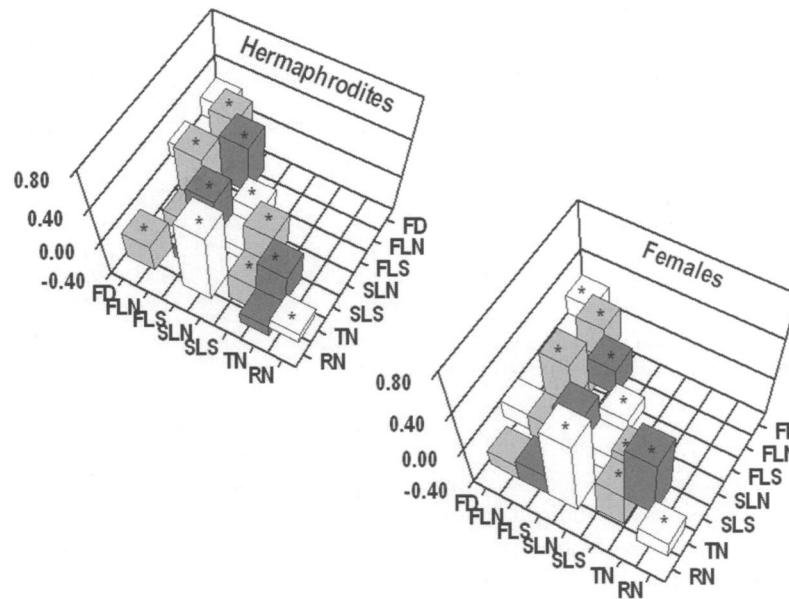


Figure 1: Significant ($P < .05$) heritabilities (*diagonal*) and genetic correlations (*left of the diagonal*) between traits within hermaphrodites and females. Parameters significant after Bonferroni adjustment for multiple tests are denoted with an asterisk. FD = flowering date; FLN = fall leaf number; FLS = fall leaf size; SLN = spring leaf number; SLS = spring leaf size; TN = trichome number; RN = runner number.

and the latter is selected to decrease ($\beta'_F = -0.0270$). Both of these contribute to the negative indirect response to selection that is about twice the size of the direct response to selection (-0.0279 vs. 0.0083). Inspection of gender-specific contributions to selection response that involve covariation between the sex morphs (e.g., $G_{HF}\beta'_F$, $G_{HF}\beta'_{Hm}$) also indicates that this type of covariation restricts direct response to selection much of the time (five of six responses; table 3).

The relative roles of all gender-specific contributions to the total predicted selection response are illustrated in figure 2. A relatively small proportion of the predicted response in hermaphrodites and females is due to selection occurring in the opposite sex morph ($G_{HF}a\beta_F$ and $G_{HF}\beta_{Hm}$, respectively). This can be seen most readily in female response, where the contribution due to selection via hermaphrodites' male fertility is usually less than 30% of the total response. The exception, however, is flowering date, where the majority (85%) of the response is due to selection occurring via male fertility of hermaphrodites. In hermaphrodites, contributions via male fertility account for 15% (flower date) to 75% (spring leaf number) of total response. In addition, despite the fact that hermaphrodites contribute only 26% of the female gametes to the next generation of hermaphrodites ($b = 0.26$), selection via female fertility of hermaphrodites contributes substantially to the total response to selection in a few traits, such as

flowering date (59%) and trichome number (31%), which were under strong selection via this fertility pathway.

Predicted Response in Sexual Dimorphism

The change in sexual dimorphism predicted for this set of traits is illustrated in figure 3. Flower date, fall leaf size, and fall leaf number lie close to the diagonal line that reflects no predicted change in sexual dimorphism. This is not surprising, because all were selected similarly (to increase or decrease) through both male and female fertilities. The off-diagonal position of the other traits indicates predicted changes in sexual dimorphism, albeit small ones. Most notable is that spring leaf number is predicted to increase two times as fast in hermaphrodites as in females (0.0510 vs. 0.0211 standard deviation units) across one generation. The predicted response in females parallels selection on spring leaf number in females ($\beta'_F = 0.0640$), whereas the response in hermaphrodites reflects the sum of all three positive gender-specific contributions (fig. 2) despite negative selection via male and female fertility in hermaphrodites. Single-generation predicted responses also suggest that spring leaf size will increase in hermaphrodites while decreasing in females (0.011 vs. -0.002 standard deviation units).

Despite the fact that predicted changes reflect small percentages per generation, if all else is equal (i.e., no op-

Table 4: Genetic correlations (SE) between the sex morphs of *Fragaria virginiana*

Female trait	Hermaphrodite trait						
	Flower date	Fall leaf number	Fall leaf size	Spring leaf number	Spring leaf size	Trichome number	Runner number
Flower date	.475 (.048) ^{a*}						
Fall leaf number	.013 (.042)	.445 (.045) ^{a*}					
Fall leaf size	.059 (.055)	-.112 (.049)	.610 (.039) ^{a**}				
Spring leaf number	.086 (.053)	.232 (.053) ^{a*}	-.180 (.048) [*]	.224 (.052) ^{a*}			
Spring leaf size	-.164 (.047) [*]	-.154 (.050) [*]	.221 (.059) ^{a**}	-.307 (.052) ^{a**}	.363 (.042) ^{a**}		
Trichome number	.013 (.067)	-.027 (.052)	-.014 (.042)	.104 (.050)	-.143 (.053) [*]	.567 (.037) ^{a**}	
Runner number	.029 (.054)	.026 (.052)	-.085 (.053)	.055 (.054)	-.165 (.049) [*]	.135 (.051) ^{a**}	.070 (.058)

Note: Correlations between homologous traits are on the diagonal, and those between nonhomologous traits are off the diagonal.

^a Parameters that remain significant after Bonferroni correction for multiple tests.

* $P < .05$.

** $.05 < P < .1$.

posing selection on other life stages) and selection/genetic variances remain stable over time, after 100 generations, females are predicted to be 64% less leafy and have 47% smaller leaves in the spring than hermaphrodites.

Discussion

Not unlike many gynodioecious plants (table 1), the minor ($\leq 6\%$) degree of sexual dimorphism in vegetative and phenological traits in *Fragaria virginiana* stands in stark contrast to the marked sexual dimorphism in reproductive traits (e.g., petal size and fruit-setting ability; Ashman 2003). The results of this study shed some of the first light on why this might be. First, although strength and direction of selection varied between fertility modes for some traits, many traits are selected similarly. Second, predicted response to selection is limited not only by low genetic variation but also by extensive genetic covariance, and covariance between traits within sex morphs appears to represent a constraint on par with that of covariance between sex morphs. Third, these constraints combine with the different modes of gamete transmission to produce very different gender-specific contributions to the next generation of females and hermaphrodites. Finally, these elements together produce predicted responses to selection that are concordant with the direction and level of dimorphism seen in a closely related dioecious species, although not with the general pattern seen in dioecious species reviewed in table 1. In the following paragraphs, I explore these results in greater detail and consider the assumptions underlying the predicted changes in sexual dimorphism.

Gender-Specific Phenotypic Selection

Theory predicts that sexual dimorphism results from divergent selection via male and female fertility (reviewed

in Geber 1999). The only evidence for divergent gender-specific selection in this study involved spring leaf number and size: selection favored numerous, small leaves via females' fertility but the reverse via male fertility, although the latter was not statistically significant (table 3). Only one plant study provides data for comparison, and it was conducted on a sexually dimorphic dioecious shrub. Specifically, Kohorn (1994) demonstrated that different vegetative morphologies benefited male versus female reproduction in *Simmondsia chinensis*: small leaves and short internodes were weakly associated with increased male success (more flowers), while large leaves and long internodes were associated with higher female success (flower buds, seed size). Kohorn (1994) concluded that dimorphism in vegetative traits was the result of divergent optimal trait values for male and female reproductive success. Unfortunately, limited data preclude drawing any general conclusions regarding the genesis of vegetative dimorphism in dioecious or gynodioecious species. Clearly, more selection gradient studies are needed to clarify the role of gender-specific selection on vegetative traits. In particular, studies of selection on vegetative traits through components of male fertility are needed. Because vegetative traits are often subsumed into a principal component that reflects overall plant size (e.g., Elle and Meagher 2000), it is not often possible to determine whether selection on vegetative traits might differ between male and female fertility. Such studies in hermaphrodite species also would provide much-needed comparative analysis. For instance, it is unknown whether vegetative traits in hermaphrodite species reflect the compromise between conflicting selections between male and female fertility, as has been predicted for floral traits (Morgan 1992).

Predicted Response: Gender-Specific Contributions

The relative weight of gender-specific contributions to total selection response differed between females and her-

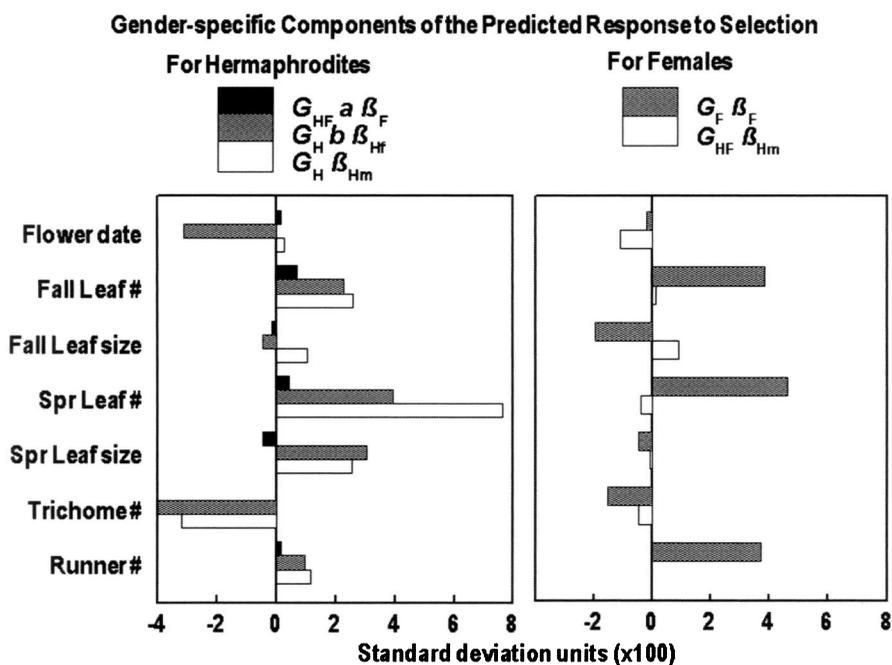


Figure 2: Gender-specific contributions to the total standardized predicted response to selection in hermaphrodite and female *Fragaria virginiana*. Gender-specific contributions are estimated as indicated in equation (2).

maphrodites. Trait means for females of the next generation are determined primarily by the female-specific contribution to total response (fig. 2) because of a preponderance of indirect components that facilitate rather than retard direct response to selection (table 3). In contrast, the male-specific contribution to female total response is small because of weaker between-sex covariance, which is further diminished by indirect responses opposing the direct responses for almost all traits. Trait means for hermaphrodites of the next generation are determined slightly more equitably by the three gender-specific contributions. Not only does each gender-specific contribution have a more equal number of antagonistic and facilitating indirect responses contributing to total response (table 3), but response to selection via female fertility of hermaphrodites contributes a large portion of the total response. These results emphasize the importance of understanding both between- and within-sex genetic covariation (e.g., Meagher 1992; Costich and Meagher 2001; Ashman 2003; Caruso et al. 2003; Delph et al. 2004) before drawing conclusions about the independent evolution of traits in the sex morphs (see also Reeve and Fairbairn 1999).

Predicted Response: Sexual Dimorphism

Predicted responses in sexual dimorphism fell loosely into two categories: those traits for which sexual dimorphism

is not expected to change and those traits for which change would be expected if all else remained constant. Little or no change in sexual dimorphism was predicted for fall leaf traits, runner number, and flowering date, and this is in line with the lack of sexual dimorphism in those traits when measured in *F. virginiana*'s dioecious sister species *Fragaria chiloensis* (Hancock and Bringhurst 1980). On the other hand, calculations presented here predict greater dimorphism in spring leaf size and number (females are predicted to produce fewer, smaller leaves than hermaphrodites). At first glance, this prediction seems contrary to the pattern seen in many dioecious species; that is, females usually have larger leaves and fewer branches (table 1). However, this trend is dominated by woody shrubs and in particular by a single genus (18 species of *Leucadendron*). Even among the three herbaceous dioecious species, *F. chiloensis* is the only one to show a trend for smaller leaves in females than in males (~10% smaller; $P = 0.12$; Hancock and Bringhurst 1980). Thus, the predicted responses for several of the traits studied here in *F. virginiana* are concordant with the direction and degree of observed sexual dimorphism in its closest dioecious relative.

Consideration of Underlying Assumptions

The predictions made here have several underlying assumptions. The first assumption is that the genetic vari-

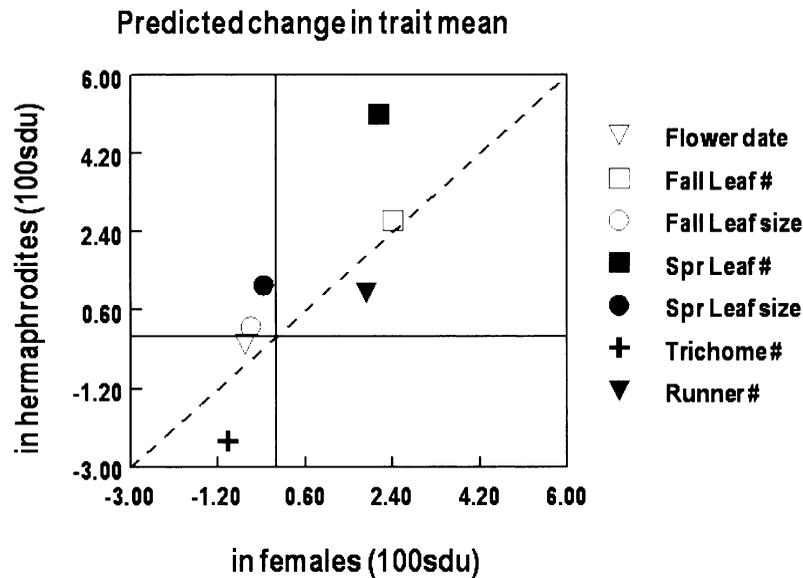


Figure 3: Predicted change in sexual dimorphism after one generation of selection on vegetative and phenological traits of *Fragaria virginiana* in a field garden. Predicted responses are shown in hundreds of standard deviation units and were calculated according to equations (1) and (2). The dashed line reflects no predicted change in sexual dimorphism.

ance-covariance matrix (G) remains constant over time (reviewed in Stepan et al. 2002). A study on reproductive traits in this species was not able to detect population differences in G for reproductive traits (Ashman 2003), and if spatial variation can be viewed as a surrogate for temporal variation, then this suggests that assuming that G is relatively constant is reasonable here. Second, predictions made here assume that the traits are not under conflicting selection pressures at other life stages or via other components of fitness (e.g., Campbell 1991; Gómez 2004) or under indirect selection via correlated traits not considered here. This latter assumption may be violated under natural pollination conditions because petal size is positively correlated with spring leaf size (T.-L. Ashman, unpublished data). If selection via pollinator preferences favors increased petal size (e.g., Ashman and Diefenderfer 2001; A. L. Case and T.-L. Ashman, unpublished manuscript), it could facilitate total response to selection in hermaphrodites but retard response in females. Pollinator-mediated selection is assumed not to have played a role here because all plants were hand pollinated, but this scenario could explain the discordance between predicted sexual dimorphism in spring leaf size in *F. virginiana* and that observed in the wild. A final assumption is that estimates of fertility used here are reasonable surrogates for actual fertility.

Conclusions

By providing an integrated study of sexual dimorphism, this work sheds first light on the genesis of modest dimorphism in vegetative traits in gynodioecious plants. This work revealed that selection, although sometimes differential, was rarely divergent through male and female fertility modes. In addition, estimation and inspection of predicted responses to selection suggest that low genetic variation and pervasive genetic covariation limit response. Together, these data suggest that limited sexual dimorphism is due to genetic covariation between traits within sex morphs modifying similar selection rather than solely to strong between sex-genetic covariation restricting divergent selection. It also demonstrates that complete information on genetic covariation, direct and indirect selection, and genetic contributions to the next generation is needed before one can fully evaluate the evolutionary dynamics of sexual dimorphism.

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