American Journal of Botany 94(10): 1716–1725. 2007.

SEXUALLY DIMORPHIC INFLORESCENCE TRAITS IN A WIND-POLLINATED SPECIES: HERITABILITIES AND GENETIC CORRELATIONS IN *SCHIEDEA ADAMANTIS* (CARYOPHYLLACEAE)[1]

STEPHEN G. WELLER,[2,4] ANN K. SAKAI,[2] THERESA M. CULLEY,[3] DIANE R. CAMPBELL,[2] PAUL NGO,[2] AND AMY K. DUNBAR-WALLIS

[2]Department of Ecology and Evolutionary Biology, University of California, Irvine, California 92697 USA; and
[3]Department of Biological Sciences, University of Cincinnati, Cincinnati, Ohio 45221-0006 USA

Sexual dimorphism may be especially pronounced in wind-pollinated species because they lack the constraints of biotically pollinated species that must present their pollen and stigmas in similar positions to ensure pollen transfer. Lacking these constraints, the sexes of wind-pollinated species may diverge in response to the different demands of pollen dispersal and receipt, depending on the magnitude of genetic correlations preventing divergence between sexes. Patterns of sexual dimorphism and genetic variation were investigated for inflorescence traits in *Schiedea adamantis* (Caryophyllaceae), a species well adapted to wind-pollination, and compared to *S. salicaria*, a species with fewer adaptations to wind pollination. For *S. adamantis*, dimorphism was pronounced for inflorescence condensation and its components, including lateral flower number and pedicel length. Within sexes, genetic correlations between traits may constrain the relative shape of the inflorescence. Correlations detected across sexes may retard the evolution of sexual dimorphism in inflorescence structure, including features favoring enhanced dispersal and receipt of pollen. Despite genetic correlations across sexes, common principal components analysis showed that genetic variance–covariance matrices (G matrices) differed significantly between the sexes, in part because of greater genetic variation for flower number in hermaphrodites than in females. G matrices also differed between closely related *S. adamantis* and *S. salicaria*, indicating the potential for divergent evolution of inflorescence structure despite general similarities in morphology and pollination biology.

Key words: genetic correlations; gynodioecy; inflorescence architecture; quantitative genetics; *Schiedea adamantis*; *Schiedea salicaria*; sexual dimorphism; wind pollination.

Secondary sex characters in flowering plants include a wide variety of traits associated with growth and reproduction (Lloyd and Webb, 1977; Delph, 1996, 2005) as well as inflorescence traits, such as flower number and position (reviewed in Geber et al., 1999). Lloyd and Webb (1977) noted that sexual dimorphism in inflorescence traits may be especially pronounced in wind-pollinated species. They argued that while biotically pollinated species must position their pollen and stigmas in similar locations to ensure pollen transfer, this constraint is absent in wind-pollinated species. The optimal positions for pollen dispersal and pollen receipt could therefore be quite different in wind-pollinated species relative to biotically pollinated species (Lloyd and Webb, 1986). Differing selective optima for pollen dispersal and receipt presumably could explain the substantial inflorescence dimorphism in some wind-pollinated species (e.g., Restionaceae, Kircher, 1986; *Ateleia herbert-smithii*, Janzen, 1989; *Buchloe dactyloides,* Quinn, 1991).

The rate at which sexual dimorphism evolves in wind-pollinated species should depend not only on selection, including that imposed by the morphological constraints associated with abiotic dispersal and receipt of pollen, but also on any underlying genetic constraints reflected in additive genetic variances and covariances (hereafter the G matrix) of the traits (Lande and Arnold, 1983). Heritable genetic variation is required for quantitative traits such as flower number to evolve. On the other hand, strong positive genetic covariances between the sexes could retard divergence of inflorescence traits in sexually dimorphic species even when divergence might improve pollen dispersal or receipt. Such genetic correlations could influence divergence between sexes in inflorescence features in biotically pollinated species (Ashman, 1999, 2003, 2005; Ashman and Hitchens, 2000), but little is known about the quantitative genetics of inflorescence features in wind-pollinated species. Without this information, predictions about the evolution of sexual dimorphism in inflorescence traits as well as other sexually dimorphic traits are difficult. Furthermore, predictions about long-term changes generally assume that the G matrix is stable over time (Lande, 1979). A review of studies of the G matrix in closely related taxa indicates that this assumption is not always met (Steppan et al., 2002), and strong selection is one of the factors that can cause changes over time (Roff and Mosseau, 1999). However, few such comparisons of the G matrix have been made in plants (e.g., Donohue et al., 2000; Waldmann and Andersson, 2000; Widén et al., 2002; Ashman, 2003) and none in closely related wind-pollinated species.

We investigated the degree of sexual dimorphism and the G matrix for inflorescence traits in gynodioecious, wind-pollinated *Schiedea adamantis* (Caryophyllaceae), and compared these values with those for closely related *S. salicaria* (Weller et al., 2006). Both species occur within a lineage of 34 species endemic to the Hawaiian Islands, of which 10 species are sexually dimorphic (Wagner et al., 2005). Inflorescences are determinate cymes with lateral dichasia or monochasia that

[1] Manuscript received 23 February 2007; revision accepted 19 August 2007.

The authors thank Y. Alliman, R. Basile, Y. Theau, and W. Yang for care of plants, and C. Fenster and R. Reynolds for suggesting a method for calculating standard errors for heritabilities. This research was supported by the National Science Foundation (DEB 9815878) with NSF REU support for P.N.

[4] Author for correspondence (e-mail: sgweller@uci.edu)

vary greatly in the degree of elongation of the internodes and the number of flowers (Wagner et al., 2005). Wind tunnel studies have been used to determine whether species are wind or biotically pollinated and to characterize traits associated with evolution of wind pollination (Weller et al., 1998). All sexually dimorphic species of *Schiedea* are wind-pollinated, although the extent of adaptation to wind pollination varies among species. Inflorescences of wind-pollinated species are much more condensed than those of biotically pollinated species, based on the ratio of flower number to inflorescence length (Weller et al., 1998).

In this study we focused on *S. adamantis,* a species well adapted to wind pollination, and *S. salicaria*, a closely related species that is wind-pollinated but has fewer adaptations to wind pollination. Our assessment of the extent of wind pollination in these species is based on pollen production and pollen size, two traits identified by stepwise discriminant analysis in an earlier study as the best indicators of wind pollination (Weller et al., 1998). *Schiedea adamantis* produces more pollen than *S. salicaria* (22 177 vs. 14 746 pollen grains per flower) and smaller pollen grains (28.7 vs. 33.5 μm; Weller et al., 1998). Given Lloyd and Webb's work (1977, 1986), we predicted that sexual dimorphism should be greater in the species with more pronounced adaptations to wind pollination. For example, greater elevation of hermaphroditic inflorescences above the foliage would result in more effective dispersal of pollen grains. Elongated pedicels of hermaphroditic flowers would project anthers beyond the boundary layer, again leading to more effective pollen dispersal. These predictions assume that strong positive genetic correlations have not prevented divergence between the sexes. Depending on the magnitude of genetic correlations across the sexes, traits associated with wind pollination that might show greater sexual dimorphism in *S. adamantis* than *S. salicaria* include inflorescence condensation, flower number, pedicel length, and the extent of elongation of the internode subtending the inflorescences.

To investigate sexual dimorphism of inflorescence traits and heritabilities and genetic correlations for these traits, we used an experimental crossing program to (1) examine sexual dimorphism in *S. adamantis*, (2) estimate the G matrix of inflorescence traits, and (3) compare these values to those obtained in a previous study of inflorescence traits in *S. salicaria* (Weller et al., 2006). Estimation of the G matrix allows predictions about the expected direction of evolution, assuming that selection for wind pollination is ongoing in these species. Our study also allowed us to investigate potential genetic correlations that might limit the extent of sexual dimorphism in traits associated with wind pollination. For this reason, we investigated the traits that underlie sexual dimorphism, rather than simply one or a few composite traits that summarize the extent of wind pollination. Because *S. adamantis* is better adapted to wind pollination than *S. salicaria*, a closely related species that is also wind pollinated (Weller et al., 1998; Nepokroeff et al., 2005; Wagner et al., 2005), we were able to test the prediction that sexual dimorphism in inflorescence traits should be more pronounced in *S. adamantis*.

MATERIALS AND METHODS

Study organism—*Schiedea adamantis* St. John is a perennial, woody shrub found in a single population in dry shrubland on the north slope of Diamond Head Crater (Oahu, Hawaii) at approximately 125 m (Wagner et al., 2005). The sole population is gynodioecious and originally contained hermaphrodites and approximately 39% females (Sakai et al., 1997) before drought from 1998–2001 eliminated all but five individuals from the natural population (A. Bakutis, Division of Forestry and Wildlife, State of Hawaii, personal communication). No native or non-native pollinators have been observed visiting *S. adamantis*, and based on comparisons to species observed in a wind tunnel (Weller et al., 1998), *S. adamantis* is clearly wind pollinated. Flowers of all *Schiedea* species are apetalous, and nectar volumes are well below those of biotically pollinated species (Weller et al., 1998; Golonka et al., 2005).

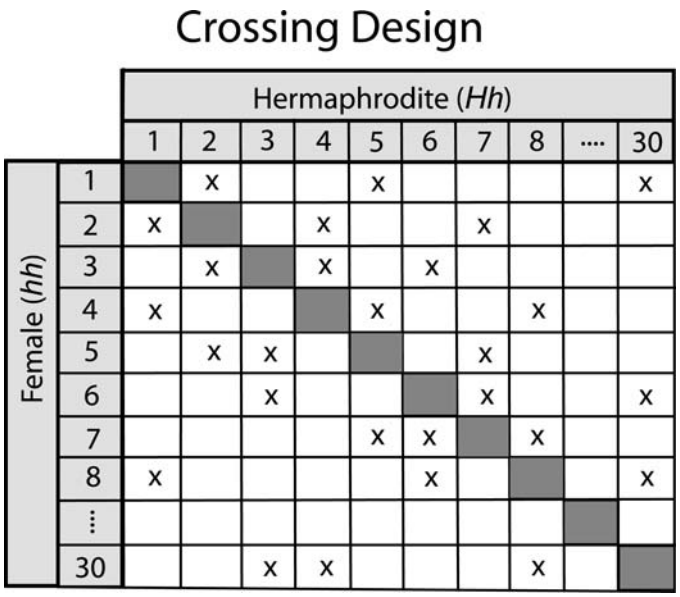

Fig. 1. Partial diallel crossing design used to estimate heritabilities in *Schiedea adamantis*. Each of 30 heterozygous hermaphrodites was used as a sire mated to three unrelated females. Inflorescence traits were measured for approximately three hermaphroditic and three female progeny from each of the 90 full sib families resulting from these crosses.

Phylogenetic analysis (Nepokroeff et al., 2005) places nine of the 10 sexually dimorphic species of *Schiedea* (of 34 species total) in a large clade containing 12 species supported at a level of 77% using bootstrap analysis. Within this clade, a sexually dimorphic subclade containing *S. adamantis*, *S. spergulina*, *S. kealiae*, *S. ligustrina*, and *S. salicaria* is supported by bootstrap analysis at a level of 70%. In this subclade *S. adamantis* and *S. salicaria* are gynodioecious, *S. kealiae* is subdioecious, and *S. spergulina* and *S. ligustrina* are dioecious.

Male sterility in *Schiedea* is controlled by a single nuclear gene (Weller and Sakai, 1991). Hermaphroditic plants are homozygous dominant (*HH*) or heterozygous (*Hh*). In the field, females are highly outcrossed and hermaphrodites are more strongly selfing (Sakai et al., 1997). Inbreeding depression is very strong, based on comparisons of selfed and outcrossed progeny (Sakai et al., 1997). In theoretical models for species with nuclear control of male sterility (Charlesworth and Charlesworth, 1978), levels of inbreeding depression and selfing rates are high enough to predict that females should increase in frequency in populations. Under field conditions, females of *S. adamantis* produce 2.3 times as many seeds as hermaphrodites, indicating that shifts in resource allocation resulting in reduced female function in hermaphrodites would maintain females in this species in the absence of inbreeding depression and high selfing of hermaphrodites (Sakai et al., 1997).

Crossing design—We used a modified partial diallel designed to measure the heritability, genetic correlations, and potential sexual dimorphism of traits associated with wind pollination (Fig. 1). This crossing program, which was similar to one that we used for *S. salicaria* in both design and sample size (Weller et al., 2006), allows direct comparisons between the species. To ensure that the progeny of *S. adamantis* would include both hermaphrodites and females, we crossed each of 30 heterozygous hermaphrodites (genotype *Hh*) from unrelated families to three unrelated females (genotype *hh*), subject to the

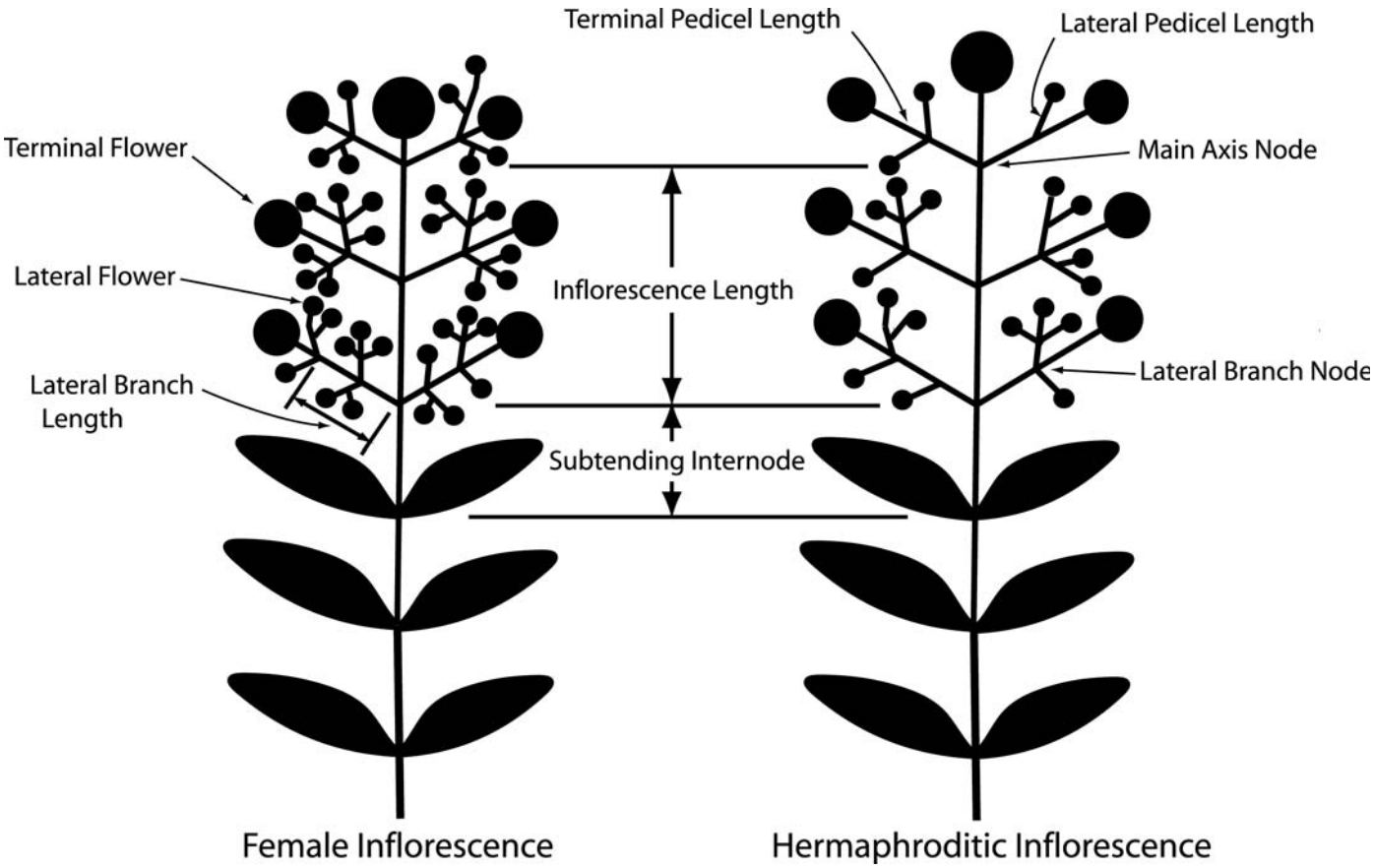

Fig. 2. Schematic diagram of female and hermaphroditic inflorescences of *Schiedea adamantis* emphasizing sexual dimorphism in lateral flower number and pedicel length of terminal and lateral flowers. The extent of inflorescence condensation (total flower number divided by the length of the inflorescence) and the proportion of flowers producing capsules following saturating pollinations also differ significantly between the sexes.

constraint that each female was also crossed with three hermaphrodites from different families. A total of 90 full sibships resulted from this crossing program. Using this design, we estimated additive genetic variances by examining the component of variation among the 30 paternal half-sib families (Kearsey, 1965; Meagher, 1992). Progeny were raised under greenhouse conditions. It was not possible to conduct the study in the field both because of the extremely steep terrain where these plants grow and the potential negative impacts on the sole population of this federally listed endangered species.

Seeds from the 90 full sibships were planted in fall 2001, and progeny were transplanted to 8-cm^2 pots in 2002 before inflorescences were measured. Liquid fertilizer (Grow More; 20-20-20 NPK plus micronutrients) was applied weekly (350–400 ppm), and plants were watered as needed. Inflorescence traits were measured between June 2002 and March 2003 for a total of 519 individuals (approximately three plants per sex for each of the 90 full sibships).

The inflorescence of *Schiedea* is a determinate, compound dichasium (Fig. 2), and flowering is initiated when the most distal flower on the main axis opens. The distal flowers on the lateral branches, referred to as terminal flowers in this paper (Fig. 2), open next, followed by the axillary, or lateral flowers. Fruits of *S. adamantis* are capsules that mature about 3 wk after pollination. Terminal and lateral flowers and capsules were analyzed separately because of distinct differences in flower size related to position in the inflorescence (cf. Diggle, 1995). We controlled for level of pollination by hand-pollinating all flowers on the two inflorescences per plant that were measured. Under field conditions, it seems unlikely that females, which produce many more capsules and seeds than hermaphrodites, are pollen limited (Sakai et al., 1997).

Heritabilities, coefficients of additive genetic variance, and genetic correlations were calculated for inflorescence traits that might diverge between the sexes in response to selection for more efficient wind pollination. Inflorescence condensation (the number of flowers divided by the length of the inflorescence in cm) and characters contributing to the degree of condensation were of special interest because condensation is a clear adaptation for wind pollination in *Schiedea* and differs between the sexes of *S. salicaria* (cf. Weller et al., 2006). Within each full sibship, three females and three hermaphrodites were measured to detect potential sexual dimorphism. Node number of the main axis was measured because of its potential relationship to total flower production. The number of nodes of the lateral branch axis was measured because flower number, a component of inflorescence condensation, is most likely related to the number of nodes. Lateral branch length was also measured because condensed inflorescences are usually narrower than diffuse inflorescences, particularly for species well adapted for wind pollination, as in *S. adamantis* (Weller et al., 1998). Pedicel lengths for two terminal and two lateral flowers were recorded because these traits influence the extent of inflorescence condensation. The length of the internode below the inflorescence was measured because many wind-pollinated species, including congeneric *S. globosa*, have inflorescences borne on elongated subtending internodes (Weller et al., 2006). We measured fruit production for terminal and lateral flowers; percentage fruit production of terminal and lateral flowers combined was analyzed following arcsine square-root conversion. Values for traits were averaged first within inflorescences when appropriate and then across the two inflorescences that were pollinated for each plant. The number of inflorescences on each plant was counted when pollinated inflorescences were harvested.

Analysis—Sexual dimorphism in inflorescence traits was investigated using both univariate and multivariate methods. For the univariate method, we used paired *t* tests to compare the paternal family means between the two sexes, paired by paternal sibship. Significance levels were adjusted for multiple comparisons using the sequential Bonferroni test. Composite traits (those traits such as total flower number that were directly based on other traits) were not

included in the Bonferroni test. As a multivariate way of describing differences between the sexes, sexual dimorphism was also investigated using MANOVA and canonical discriminant analysis. Composite traits (inflorescence condensation, total flower and capsule number, proportion of flowers producing capsules) were not used in the multivariate analyses to avoid using a trait twice.

Additive genetic variance, narrow-sense heritability, and additive genetic covariance were estimated by examining the components of variation among paternal half-sib families (see Kearsey, 1965; Shaw, 1987; Meagher, 1992; Culley et al., 2006; Weller et al., 2006). Values were estimated separately for the hermaphroditic and female progeny using Proc Mixed in SAS version 9.1 (SAS Institute, 2002–2003). The model included effects of paternal parent, maternal parent (both specified as random factors because the original parental plants were a random subset of genotypes in the natural population), and a residual error term. We did not include an interaction between the paternal and maternal parent because the large number of missing cells in a partial diallel would complicate its interpretation (Searle, 1992). A preliminary analysis including such a term detected a significant interaction for only one trait. We obtained standard errors for the heritability estimates using Proc Iml in SAS following code given by Holland et al. (2003). Their code implements the delta method for finding approximate standard errors for heritabilities based on variance components.

Significance of the paternal effect was tested using a log likelihood ratio test to compare the full model with a reduced model containing only the maternal parent effect and residual error (Littell et al., 1996). A significant effect of the paternal half-sibship indicates significant additive genetic variance (Lynch and Walsh, 1998). Additive genetic variance (V_A) was estimated for each trait in females and in hermaphrodites by multiplying the paternal variance component by four (Falconer and Mackay, 1996). Narrow-sense heritabilities were calculated for each trait in each sex as the additive genetic variance divided by the total variance. Significance levels for heritability estimates were reported without adjusting for multiple tests (see justification in Moran, 2003; Verhoeven et al., 2005) and were also reported using the sequential Bonferroni method (Sokal and Rohlf, 1995).

Genetic covariances and correlations were estimated separately for females and hermaphrodites, using best linear unbiased predictors (BLUPs) of sire breeding values obtained from our Proc Mixed analysis (SAS Inc., 2002–2003; Conner et al., 2003). Pearson correlation coefficients between BLUPs and their confidence limits based on Fisher's z transformation were calculated for each sex using Proc Corr in SAS. For examining genetic correlations across sexes, the female and hermaphroditic data sets were combined, and Pearson correlation coefficients were calculated between homologous traits of the two sexes. A genetic correlation between sexes substantially less than one would indicate some genetic variance for trait dimorphism (Lynch and Walsh, 1998). Correlations are provided for traits with significant heritabilities ($P < 0.05$, before Bonferroni correction). To facilitate comparison with *S. salicaria*, we provide correlations for several traits with nonsignificant heritabilities in *S. adamantis* but with significant heritability in *S. salicaria*. Significance levels for genetic correlations were also adjusted using the sequential Bonferroni method for multiple comparisons, although this approach is likely to result in type II errors (failure to detect a true difference; Moran, 2003; Verhoeven et al., 2005). Use of uncorrected P values is noted in the results.

We compared the G matrices of the sexes with respect to genetic variances and covariances. The matrix entries were estimated from covariances between the BLUPs for the sire breeding values obtained from the Proc Mixed analysis (the same BLUP values were used to obtain genetic covariances and correlations). Comparison of the matrices utilized common principal components analysis (jump-up approach of CPC; Phillips, 1998; Phillips and Arnold, 1999), perhaps the most widely used method for comparing G matrices (Houle et al., 2002; Mezey and Houle, 2003). We were unable to use CPCrand, an alternative method that does not make restrictive assumptions about normality and that can incorporate error in estimation of individual values, because that program does not accommodate our breeding design. The CPC method can reveal whether the matrices are equal, proportional (indicating similar structures of genetic covariation but with one sex having proportionally higher genetic variance), share common eigenvectors (but without overall variation differing by a constant), or are unrelated. For this analysis, we included seven traits (inflorescence length, length of the internode subtending the inflorescence, lateral flower number, pedicel length of terminal flowers, pedicel length of lateral flowers, lateral branch length, and total inflorescence number) that had non-zero estimates of heritabilities for at least one of the sexes and that were not composites (e.g., total flower number, proportion of flowers producing capsules) of other traits or strongly related to other traits (terminal and lateral capsule numbers). Removal of these traits was required to produce matrices with positive eigenvalues amenable to analysis with CPC. We also used CPC to compare the G matrices based on BLUPs for both sexes of *S. adamantis* to those of both sexes of *S. salicaria* (Weller et al., 2006). In addition, we compared the two species with respect to the genetic correlations (based on BLUP values) for particular trait pairs using Fisher's z transformation to test for a significant difference (SAS Inc., 2002–2003). This procedure helped to identify underlying causes for differences detected using CPC.

RESULTS

Sexual dimorphism of inflorescence traits—Inflorescences of *Schiedea adamantis* were sexually dimorphic in a number of traits related to wind pollination (Table 1). Although females and hermaphrodites had similar inflorescence lengths, females had more condensed inflorescences than did hermaphrodites ($P = 0.008$, Table 1, unadjusted probability; Fig. 2) because females produced significantly more lateral flowers (Table 1). Pedicel lengths of hermaphrodites were longer than those of females for both terminal and lateral flowers (Table 1; Fig. 2). Females produced more terminal and lateral capsules than did hermaphrodites (Table 1), and a greater proportion of female flowers produced capsules ($P < 0.001$, Table 1, unadjusted values). Using a multivariate approach, we also found significant differences between females and hermaphrodites (MANOVA, Wilk's $\lambda = 0.0433$; $F_{12,18} = 33.14$; $P < 0.0001$). The canonical discriminant function was highly, positively correlated with terminal and lateral capsule number (correlation coefficients = 0.50 and 0.64, respectively), and highly, negatively correlated with terminal and lateral pedicel length (correlations coefficients = −0.85 and −0.87, respectively), suggesting that females differ from hermaphrodites primarily in having more capsules and shorter pedicels.

Heritabilities of inflorescence traits—Inflorescence condensation, a key feature associated with wind pollination, did not have significant heritability in either females or hermaphrodites (Table 2). On the other hand, length of the internode subtending the inflorescence, also associated with wind pollination, did have significant heritable variation in females, as did several other traits that can alter the inflorescence structure and contribute to inflorescence condensation. In females, these traits include pedicel lengths of terminal and lateral flowers, and lateral branch length, although only pedicel length of lateral flowers was significant after a Bonferroni correction. Genetic variation for the length of the inflorescence was marginally significant for females ($P = 0.088$). In hermaphrodites, number of lateral flowers, pedicel length of terminal flowers, and lateral branch length had significant heritabilities. Following Bonferroni correction, no heritabilities were significant for hermaphrodites.

Genetic correlations of inflorescence traits—Significant genetic correlations of heritable traits were relatively uncommon, although strong genetic correlations were found for a number of traits with relatively high, though nonsignificant, heritabilities (Tables 3 and 4). Among those female traits with significant heritabilities, inflorescence length was positively correlated with the length of the internode subtending the inflorescence as well as with the length of the lateral branch. Pedicel lengths of terminal and lateral flowers were correlated, and pedicel length of terminal flowers was positively correlated with lateral branch length (Table 3). Lateral branch length and node number were also correlated for females. Within

TABLE 1. Means of inflorescence traits for females and hermaphrodites of *Schiedea adamantis*. The sample size (number of paternal half sibships) was 30 for all traits. Differences between female and male traits were evaluated using paired *t* tests (for proportion of flowers producing fruits, values were arcsine square-root transformed). All significant differences remained significant after application of a sequential Bonferroni test (shown by asterisk and based on 12 traits; inflorescence condensation, total flower and capsule number, and proportion of flowers producing capsules, all composite traits, were not included in the Bonferroni adjustment, although even with their inclusion, all differences were significant with the exception of inflorescence condensation).

Trait	Females Mean (SE)	Hermaphrodites Mean (SE)	*t*	*P*
Inflorescence condensation	15.682 (0.500)	14.223 (0.423)	2.87	0.008
Length of pollinated inflorescences (cm)	6.499 (0.144)	6.373 (0.140)	0.86	0.398
Inflorescence node no.	3.341 (0.038)	3.297 (0.043)	1.16	0.257
Length of internode subtending inflorescence (cm)	4.102 (0.076)	4.054 (0.066)	0.63	0.536
No. of terminal flowers	7.640 (0.0790)	7.556 (0.081)	1.09	0.284
No. of terminal capsules	7.581 (0.0830)	7.100 (0.0893)	5.43	<0.0001*
No. of lateral flowers	89.291 (2.907)	78.750 (2.569)	3.48	0.0016*
No. of lateral capsules	84.231 (2.833)	65.091 (2.078)	6.90	<0.0001*
Pedicel length of terminal flowers (cm)	0.789 (0.015)	1.023 (0.020)	13.86	<0.0001*
Pedicel length of lateral flowers (cm)	0.538 (0.014)	0.751 (0.016)	16.2	<0.0001*
Lateral branch length (cm)	1.607 (0.042)	1.560 (0.039)	1.16	0.256
No. of nodes on lateral branch	1.078 (0.012)	1.055 (0.010)	1.36	0.184
Total inflorescences	8.431 (0.293)	8.847 (0.339)	1.32	0.196
Total flowers	96.931 (2.927)	86.325 (2.585)	3.49	0.0016
Total capsules	91.813 (2.860)	72.277 (2.089)	7.01	<0.0001
Proportion of flowers producing capsules	0.943 (0.006)	0.850 (0.010)	9.69	<0.0001

hermaphrodites, inflorescence condensation was positively correlated with lateral flower number (Table 4). As in females, inflorescence length was also positively correlated with lateral branch length (Table 4). Lateral flower number was negatively correlated with the proportion of flowers producing fruits. As in the case of females, pedicel lengths of terminal and lateral hermaphroditic flowers were positively correlated, and pedicel length of terminal flowers was positively correlated with lateral branch length.

Several inflorescence traits had positive genetic correlations across sexes. Inflorescence length was positively correlated across sexes ($r = 0.458$, $P = 0.0109$, 95% confidence intervals $= 0.118, 0.703$). Terminal and lateral pedicel lengths were both positively correlated across sexes ($r = 0.506$, $P = 0.0043$, 95% confidence intervals $= 0.179, 0.733$; and $r = 0.638$, $P = 0.0001$, 95% confidence intervals $= 0.361, 0.812$, respectively), and terminal pedicel length in hermaphrodites was positively correlated with lateral pedicel length and lateral branch length in females ($r = 0.532$, $P = 0.0025$, 95% confidence intervals $= 0.212, 0.749$; and $r = 0.464$, $P = 0.0098$, 95% confidence intervals $= 0.124, 0.706$, respectively). Lateral branch length ($r = 0.495$, $P = 0.005$, 95% confidence intervals $= 0.164, 0.726$) and total inflorescence number ($r = 0.456$, $P = 0.0112$, 95% confidence intervals $= 0.115, 0.701$) were correlated across the sexes. All these correlations were substantially less than one, indicating the existence of some genetic variance for sexual dimorphism between homologous traits across the sexes.

Significant differences between the G matrices occurred for the two sexes, a finding consistent with genetic correlations less than one. The CPC analysis indicated that G matrices for

TABLE 2. Narrow-sense heritabilities (SE) of inflorescence traits in females and hermaphrodites of *Schiedea adamantis*. Asterisks indicate heritabilities significant at the 0.05 level after a sequential Bonferroni test (two composite traits, inflorescence condensation and proportion of flowers producing fruits, were not included in the Bonferroni correction). CV_A is the coefficient of additive genetic variance. χ^2 is the test statistic associated with the log likelihood ratio test for an effect of the paternal parent.

	Females				Hermaphrodites			
Trait	h^2 (SE)	χ^2	*P*	CV_A	h^2	χ^2	*P*	CV_A
Inflorescence condensation	0.253 (0.195)	2.5	0.114	19.74	0.199 (177)	1.9	0.655	17.10
Length of pollinated inflorescences	0.263 (0.191)	2.9	0.088	13.93	0.256 (0.196)	2.5	0.114	13.95
No. of nodes on inflorescence axis	0.114 (0.170)	0.6	0.439	5.24	0.00 (0)	0	1	4.73
Length of internode subtending inflorescence	0.281 (0.173)	4.6	0.032	11.95	0.247 (0.173)	3.2	0.074	11.14
No. of terminal flowers	0.160 (0.178)	1.1	0.294	5.53	0 (0)	0	1	0
No. of terminal capsules	0.195 (0.183)	1.6	0.206	6.40	0.008 (0.141)	0	1	1.53
No. of lateral flowers	0.142 (0.176)	0.8	0.371	16.28	0.372 (0.206)	5.7	0.017	25.8
No. of lateral capsules	0.192 (0.182)	1.5	0.221	19.64	0.119 (0.159)	0.7	0.403	16.2
Pedicel length of terminal flowers	0.328 (0.193)	5.0	0.025	13.95	0.433 (0.222)	6.8	0.009	13.59
Pedicel length of lateral flowers	0.469 (0.218)	8.9	0.003*	21.30	0.316 (0.206)	3.8	0.051	14.52
Lateral branch length	0.410 (0.219)	6.0	0.014	19.30	0.419 (0.220)	6.3	0.012	19.24
No. of nodes on lateral branch	0.022 (0.132)	0	1	2.48	0 (0)	0	1	0
Total inflorescences	0.046 (0.142)	0.2	0.655	11.05	0.056 (0.172)	0.1	0.752	11.83
Proportion of flowers producing capsules	0.176 (0.166)	1.6	0.206	4.65	0.059 (0.149)	0.1	0.752	4.36.11

TABLE 3. Estimates of genetic correlations (r, 95% confidence intervals, P) for females of *Schiedea adamantis* using best linear unbiased predictors (BLUPs) of sire breeding values obtained from the Proc Mixed analysis. Traits listed are those with significant heritabilities ($P < 0.05$; uncorrected) in *S. adamantis* (designated with one asterisk) or traits with significant heritabilities in closely related *S. salicaria* (Weller et al., 2006). Correlations of those traits in *S. adamantis* with $P < 0.05$ are shown in the third column (correlations significant after application of a sequential Bonferroni test are indicated by two asterisks). In *S. adamantis*, correlations are based on 30 paternal half-sibship families. For comparative purposes, correlations for the same trait combinations in *S. salicaria* are shown (fourth column), and the P value (uncorrected) for testing whether the correlations differ between the species (fifth column). Fruit production was not measured in *S. salicaria* because virtually all pollinated flowers produced fruits.

Trait in females	Correlated trait in females	r (95% confidence intervals), P for *S. adamantis*	r for *S. salicaria*	P for between species comparison
Inflorescence condensation	No. of lateral flowers	0.724 (0.492, 0.860), <0.0001**	0.715	0.941
Length of pollinated inflorescence	Length of internode subtending inflorescence*	0.438 (0.092, 0.689), <0.0156	0.821	0.0081
Length of pollinated inflorescence	No. of nodes on main axis	0.682 (0.426, 0.837), <0.0001**	0.498	0.2753
Length of pollinated inflorescence	No. of terminal flowers	0.667 (0.419, 0.834), <0.0001**	0.187	0.0151
Length of pollinated inflorescence	Terminal pedicel length	0.409 (0.057, 0.670), 0.0250	0.098	0.1985
Length of pollinated inflorescence	Lateral branch length*	0.362 (0.002, 0.639), 0.0495	0.735	0.0318
Length of pollinated inflorescence	Proportion of flowers producing fruits	0.371 (0.013, 0.643), 0.0426	—	—
No. of nodes on main axis	No. of terminal flowers	0.993 (0.985, 0.997), <0.0001**	0.275	<0.0001
No. of nodes on main axis	Proportion of flowers producing fruits	0.452 (0.110, 0.699), 0.0121	—	—
No. of terminal flowers	Proportion of flowers producing fruits	0.445 (0.101, 0.694), 0.0137	—	—
No. of nodes on lateral branch	No. of lateral flowers	0.374 (0.015, 0.647), 0.0420	0.000	0.133
Pedicel length of terminal flower*	Pedicel length of lateral flowers*	0.842 (0.691, 0.922), <0.0001**	0.037	<0.0001
Pedicel length of terminal flower*	Lateral branch length*	0.422 (0.073, 0.680), 0.0202	−0.024	0.0697
Lateral branch length*	No. of nodes on lateral branch	0.520 (0.194, 0.740), 0.0034	−0.118	0.0081

the two sexes shared common principal components, suggesting that the combination of traits summarizing the structure is similar between sexes. At the same time, CPC indicated that the matrices were not equal and differed in more than only a proportionality constant ($P < 0.01$). This result suggests that the differences were not confined to a simple multiplier of the overall level of genetic variance and covariances, but instead that the relative level of variation in the two sexes differed among the principal components (or eigenvectors). The first common eigenvector reflected mostly a high loading on lateral flower number, with an associated eigenvalue much higher (indicating more genetic variation in that direction) for hermaphrodites than females (46.4 vs. 12.2). The second eigenvector loaded heavily on inflorescence length with more similar eigenvalues for the sexes (0.072 vs. 0.077).

Comparison of genetic variation in S. adamantis and S. salicaria—For both sexes, the overall structure of the G matrix was quite different between *S. adamantis* and *S. salicaria*. The CPC analyses rejected hypotheses of any shared principal component, proportionality, and equality (all $P < 0.05$ in jump-up approach). One of the most striking differences between the species occurred for the genetic correlation between terminal and lateral pedicel length (Table 3). Strong positive correlations occurred for both sexes of *S. adamantis* (Tables 3 and 4), while for *S. salicaria*, correlations were close to zero or negative (species differences, uncorrected $P < 0.0001$). Hermaphrodites of *S. salicaria* had higher estimates for narrow-sense heritabilities than did *S. adamantis* hermaphrodites for 12 of the 13 traits measured for both species (Tables 2 and 5). The one exception was lateral branch length, which had significant heritabilities for both sexes in *S. adamantis* (Table 2) but not in *S. salicaria* (Table 5). Such a consistent pattern across species was not seen for females, in which lateral flower and capsule number of *S. salicaria* had high heritabilities relative to *S. adamantis*, whereas the reverse pattern occurred for pedicel length of terminal and lateral flowers of females (compare Tables 2 and 5).

TABLE 4. Estimates of genetic correlations (r, 95% confidence intervals, P) for hermaphrodites of *Schiedea adamantis* using best linear unbiased predictors (BLUPs) of sire breeding values obtained from the Proc Mixed analysis. Traits listed are those with significant heritabilities ($P < 0.05$; uncorrected) in *S. adamantis* (designated with one asterisk) or traits with significant heritabilities in closely related *S. salicaria* (Weller et al., 2006). Correlations of those traits in *S. adamantis* with $P < 0.05$ are shown in the third column (correlations significant after application of a sequential Bonferroni test are indicated by two asterisks). In *S. adamantis*, correlations are based on 30 paternal half-sibship families. For comparative purposes, shown are correlations for the same trait combinations in *S. salicaria* (fourth column) and the P value (uncorrected) for testing whether the correlations differ between the species (fifth column). Fruit production was not measured in *S. salicaria* because virtually all pollinated flowers produced fruits.

Trait in hermaphrodites	Correlated trait in hermaphrodites	r (95% confidence limits), P for *S. adamantis*	r for *S. salicaria*	P for between species comparison
Inflorescence condensation	No. of lateral flowers*	0.769 (0.565, 0.884), <0.0001**	0.619	0.260
Inflorescence condensation	Proportion of flowers producing fruits	−0.506 (−0.733, −0.178), 0.0044	—	—
Length of pollinated inflorescence	Length of internode subtending inflorescence	0.670 (0.408, 0.830), <0.0001**	0.670	0.996
Length of pollinated inflorescence	Lateral branch length*	0.419 (0.0693, 0.677), 0.0212	0.786	0.019
No. of lateral flowers*	Proportion of flowers producing fruits	−0.421 (−0.678, −0.072), 0.0205	—	—
No. of terminal capsules	Lateral branch length*	−0.374 (−0.647, −0.016), 0.0420	—	—
No. of total inflorescences	Proportion of flowers producing fruits	−0.370 (−0.644, −0.011), <0.0443	—	—
Pedicel length of terminal flowers*	Pedicel length of lateral flowers*	0.792 (0.604, 0.897), <0.0001**	−0.266	<0.0001
Pedicel length of terminal flowers*	Lateral branch length*	0.585 (0.286, 0.781), 0.0007	0.041	0.0158

TABLE 5. Narrow-sense heritabilities (SE) of inflorescence traits in females and hermaphrodites of *Schiedea salicaria* (from Weller et al., 2006; inflorescence condensation heritabilities are corrected values, although χ^2 and *P* values are unchanged). Asterisks indicate heritabilities significant at the 0.05 level after a sequential Bonferroni test. CV_A is the coefficient of additive genetic variance. χ^2 is the test statistic associated with the log likelihood ratio test for an effect of the male parent.

	Females				Hermaphrodites			
Trait	h^2 (SE)	χ^2	*P*	CV_A	h^2	χ^2	*P*	CV_A
Inflorescence condensation	0.580 (0.255)	10.4	0.0013*	28.09	0.489 (0.222)	8.9	0.0029*	30.68
Length of pollinated inflorescences	0.274 (0.184)	3.5	0.0614	16.93	0.493 (0.217)	10.4	0.0013*	23.23
No. of nodes on inflorescence axis	0.049 (0.186)	0.1	0.7518	3.26	0.415 (0.207)	7.0	0.0082	9.45
Length of internode subtending inflorescence	0.507 (0.233)	8.9	0.0029*	24.06	0.602 (0.247)	12.2	0.0005*	25.11
No. of terminal flowers	0.020 (0.178)	0.5	0.4795	2.01	0.359 (0.198)	5.6	0.0180	7.99
No. of terminal capsules	0 (0)	0	1	0	0.386 (0.201)	6.4	0.0114	8.19
No. of lateral flowers	0.601 (0.269)	10.0	0.0016*	35.29	0.668 (0.244)	15.3	<0.0001*	42.26
No. of lateral capsules	0.656 (0.275)	11.9	0.0006*	36.88	0.681 (0.246)	15.7	<0.0001*	42.04
Pedicel length of terminal flowers	0.109 (0.173)	0.50	0.4795	9.33	0.789 (0.263)	5.7	0.01696	22.73
Pedicel length of lateral flowers	0.325 (0.212)	3.6	0.0578	18.17	0.472 (0.223)	8.6	0.00336*	19.84
Lateral branch length	0.064 (0.164)	0.10	0.7518	16.34	0.262 (0.192)	2.8	0.09426	36.20
No. of nodes on lateral branch	0 (0)	0	1	0	0.033 (0.134)	0.10	0.7518	6.64
Total inflorescences	0.262 (0.212)	2.10	0.1473	27.53	0.680 (0.261)	12.3	0.00045*	44.17
Vegetative height of plant at time of first flowering	0.006 (0.142)	0	1	2.47	0.267 (0.196)	2.6	0.1069	15.11
Length of first inflorescence	0.451 (0.206)	9.20	0.0024*	27.12	0.107 (0.167)	0.4	0.5271	12.97
Plant height at time of first flowering	0.110 (0.155)	0.70	0.4028	9.59	0.147 (0.174)	0.90	0.3428	9.79

DISCUSSION

Sexual dimorphism and wind pollination—Sexual dimorphism in inflorescence traits leading to more effective dispersal and receipt of pollen might be expected in species well adapted to wind pollination, unless genetic correlations limit the extent of divergence between sexes. All sexually dimorphic species of *Schiedea* are wind pollinated and therefore might be expected to have significant sexual dimorphism in inflorescence traits associated with wind pollination. Sexual dimorphism should be greatest for those species with the most pronounced adaptations for wind pollination. Among *Schiedea* species, *S. adamantis* is particularly well adapted for wind pollination, through production of abundant, small pollen grains and highly condensed inflorescences (Weller et al., 1998; Golonka et al., 2005). A number of inflorescence traits associated with wind pollination have substantial sexual dimorphism in *S. adamantis*, in line with Lloyd and Webb's (1977, 1986) predictions for abiotically pollinated species.

Divergence between the sexes of *S. adamantis* is significant for inflorescence condensation, a key feature associated with wind pollination (Fig. 2, Table 1). Because inflorescence lengths are similar for the two sexes, differences in inflorescence condensation result solely from the greater flower production of females. Lateral branch lengths and number of nodes per lateral branch are similar for the sexes, suggesting that the greater lateral flower production of females must result from either greater flower production at nodes or perhaps greater branching. Overall dimensions of the inflorescences are different because both terminal and lateral flowers have significantly longer pedicels in hermaphrodites than in females, and the stamens of hermaphroditic flowers extend well beyond the sepals. Extension of flowers of hermaphrodites outside the boundary layer surrounding the inflorescence may be especially important for dispersal of pollen (Friedman and Harder, 2004, 2005). Similarly, the longer stigmas of females of dimorphic species compared to hermaphroditic species (Golonka et al., 2005) probably facilitate pollen capture.

Smaller flower size of female flowers of *S. adamantis* may facilitate production of more flowers per inflorescence in contrast to hermaphroditic individuals, where spatial interference between the larger hermaphroditic flowers is likely. In general, female flowers of dimorphic *Schiedea* species are smaller than hermaphroditic or male flowers because of smaller sepal size and the absence of functional anthers (Golonka et al., 2005). The shortened pedicels of female flowers may permit greater flower production per inflorescence without leading to interference between flowers. These arguments suggest that shortened pedicel length and greater flower production in females are derived traits, which is reasonable in view of the presumably recent evolution of sexual dimorphism in many species of *Schiedea* (Wagner et al., 2005). It is also plausible, however, that as wind pollination has evolved in sexually dimorphic species, longer pedicel lengths have evolved in hermaphrodites because this trait could increase the effectiveness of pollen dispersal.

Heritabilities and genetic correlations—Most inflorescence traits in *S. adamantis* had low to moderate narrow-sense heritability, despite clear differences in inflorescence structure between closely related species and despite the likelihood that these differences have a genetic basis. Inflorescence traits critical for determining the degree of inflorescence condensation (flower number and inflorescence length; Weller et al., 2006), as well as the position of the inflorescence above the foliage, a feature promoting wind pollination (Proctor et al., 1996), did have significant or nearly significant narrow-sense heritability, suggesting that selection on these traits would lead to a positive response. The positive genetic correlations between inflorescence length and the length of the subtending internode in both sexes of *S. adamantis* may be partially responsible for the overall architecture of this species. In contrast to the architecture of *S. salicaria*, which has more elongate inflorescences borne above the foliage boundary (Fig. 3), the inflorescences of *S. adamantis* are supported on short internodes at the foliage boundary of these compact shrubs. Lateral branch length, an important component of inflorescence condensation in wind-pollinated species, had heritable varia-

Fig. 3. Inflorescences of hermaphroditic individuals of *Schiedea adamantis* (left) and *S. salicaria* (right), showing the characteristic greater inflorescence condensation of *S. adamantis* relative to *S. salicaria*. Although both species are wind pollinated, *S. adamantis* has more pronounced adaptations to wind pollination, including greater pollen production and smaller pollen size.

tion in both sexes of *S. adamantis*, in contrast to *S. salicaria*. Relative to *S. adamantis*, it may have been more difficult to detect heritable variation in length of lateral branches in *S. salicaria* because of greater phenotypic plasticity.

The low heritabilities for inflorescence traits in *S. adamantis* hermaphrodites may result from depletion of additive genetic variation associated specifically with continued selection for wind pollination. An alternative explanation for low heritabilities is the loss of additive genetic variation during the genetic bottleneck that occurred when *S. adamantis* colonized Diamond Head Crater, the only known locality for this species (Wagner et al., 2005). Sexually dimorphic species of *Schiedea* typically have high levels of genetic variation, but *S. adamantis* is depleted in allozyme variation relative to other sexually dimorphic species (Weller et al., 1996). Despite the reduction in allozyme diversity, quantitative genetic variation is typically far less susceptible to the effects of population bottlenecks than allozyme variation (Lande, 1988), and it seems unlikely that the history of this population explains the reduced quantitative genetic variation for inflorescence traits.

Heritabilities of inflorescence traits of females and hermaphrodites of *S. adamantis* were similar, and the G matrices shared some principal components, although they were not equal. In contrast, there were fewer similarities in the G matrices of the sexes of *S. salicaria* (Weller et al., 2006). For both sexes of the two species, the G matrices were unrelated between species as judged by CPC analysis. This result must be interpreted cautiously, in part because a difference in one eigenvector can cause all models of similarity to be rejected (Houle et al., 2002). The result does not mean there are no similarities between the matrices (Steppan et al., 2002), but it does suggest divergence beyond a general change in the level of genetic variance. One example of these differences is the striking divergence between the species in correlation between terminal and lateral pedicel length. In *S. salicaria*, which has relatively less condensed inflorescences, correlations were close to zero or negative, while in *S. adamantis*, which has relatively more condensed inflorescences, the correlations were positive, perhaps because of the space constraints imposed by the greater condensation. Differences in heritabilities and additive genetic variance of *S. adamantis* and *S. salicaria* could in principle be due either to strong selection in the past or to differences in population size. Selection has been invoked for differences in G matrices between other closely related plant species (Waldmann and Andersson, 2000).

Resource allocation patterns in S. adamantis and S. salicaria—Females of *S. adamantis* produced more capsules

per inflorescence than hermaphrodites, and a greater proportion of flowers of females produced capsules. The negative genetic correlation between lateral flower number and the proportion of flowers producing fruits in hermaphrodites suggests resource limitations in this sex, perhaps due to stamen production, that do not occur in females. Under field conditions, differences in capsule production between the sexes of *S. adamantis* were the primary cause of the much greater seed production of females relative to hermaphrodites (Sakai et al., 1997). The greater flower number, increased proportion of flowers producing capsules, and greater seed mass of capsules of females of *S. adamantis* could result from reallocation of resources from stamens to female function (Sakai et al., in press). In the greenhouse, more flowers were also found in female vs. hermaphroditic inflorescences of *S. salicaria*, although there were no differences between sexes in capsule production (Weller et al., 2006). In the field, no differences were found for flower or capsule production between the sexes of *S. salicaria* (Weller and Sakai, 2005). The similarity under field conditions in flower and capsule production of *S. salicaria*, which has only 12–13% females in populations, argues against the importance of reallocation of resources during the initial steps in the evolution of sexual dimorphism.

Reduction in female function of hermaphrodites of *S. adamantis* relative to *S. salicaria* is consistent with the higher female frequency of *S. adamantis* (39% vs. 12–13% in *S. salicaria*). If the evolution of dioecy from gynodioecy is determined in part by the reduction in capsule production in hermaphrodites, additive genetic variation for capsule production is expected in the early stages of this transition. Despite this prediction, heritability for the proportion of flowers producing capsules was not significant ($h^2 = 0.067$, $P = 0.655$), possibly because the high levels of nutrients and water in the greenhouse environment obscured differences among the paternal half sibships. Under field conditions, the difference in seed production (females produced 2.3 times more seeds than hermaphrodites; Sakai et al., 1997) is far greater than in the greenhouse where females produced ca. 1.3 times the number of seeds as hermaphrodites (A. K. Sakai and S. G. Weller, unpublished data). These results indicate that under more stressful conditions heritabilities might have been detected more readily, although higher heritabilities would generally be expected under more uniform greenhouse environments.

Limits to sexual dimorphism in inflorescence structure—For wind-pollinated species, Lloyd and Webb (1986) noted that optimal positions for pollen dispersal and receipt may differ, and these differences could contribute to the pronounced sexual dimorphism seen in some wind-pollinated species (e.g., Restionaceae, Kircher, 1986; *Ateleia*, Janzen, 1989; *Buchloe*, Quinn, 1991). Absence of such marked sexual differentiation in species of *Schiedea* where wind pollination is particularly well developed (*S. adamantis* and *S. globosa*) suggests that selection has favored similar inflorescence features in both sexes. The G matrices of the two sexes in *S. adamantis* appear to have a common structure, differing only in the amounts of genetic variation associated with each principal component. Given the theoretical modeling by Mezey and Houle (2003), our findings suggest that there are common modules, in which different alleles affect lateral flower number and inflorescence length, and that these effects are consistent across the sexes. This result is consistent with the lack of detectable genetic correlation between lateral flower number and inflorescence length within both sexes ($P > 0.05$) and suggests that these two traits could evolve independently to adjust the level of inflorescence condensation in a particular species.

In contrast, genetic correlations between the sexes for other traits might slow the evolution of sexually dimorphic inflorescences. Correlations across sexes between inflorescence length and lateral branch length, could contribute to similarly shaped inflorescences in both sexes. Correlations across sexes between inflorescence length and the length of the subtending internode would lead to inflorescences located at the outer surface of the plant for both sexes. None of the inflorescence–trait correlations, however, are strong enough to completely prevent independent evolution of the traits. The patterns of genetic variation and covariation for *S. adamantis* and *S. salicaria* have diverged more than for the sexes of *S. adamantis*, as indicated by the structure of their G matrices. G matrices between related species of flowering plants have rarely been compared (Waldmann and Andersson, 2000), and their general stability over evolutionary time is unknown. The divergence in structure between these two species of *Schiedea* suggests the potential for divergent evolutionary trajectories in response not only to differences in selection, but also to differences in the pattern of genetic covariation. The diversity of inflorescence architecture in wind-pollinated species of *Schiedea* appears to be associated with substantial modification of G matrices during the course of adaptive radiation.

LITERATURE CITED

ASHMAN, T.-L. 1999. Quantitative genetics of floral traits in a gynodioecious wild strawberry *Fragaria virginiana*: implications for the independent evolution of female and hermaphrodite floral phenotypes. *Heredity* 83: 733–741.

ASHMAN, T.-L. 2003. Constraints on the evolution of males and sexual dimorphism: field estimates of genetic architecture of reproductive traits in three populations of gynodioecious *Fragaria virginiana*. *Evolution* 57: 2012–2025.

ASHMAN, T.-L. 2005. The limits on sexual dimorphism in vegetative traits in a gynodioecious plant. *American Naturalist* (Supplement) 166: S5–S16.

ASHMAN, T.-L., AND M. S. HITCHENS. 2000. Dissecting the causes of variation in intra-inflorescence allocation in a sexually polymorphic species, *Fragaria virginiana* (Rosaceae). *American Journal of Botany* 87: 197–204.

CHARLESWORTH, B., AND D. CHARLESWORTH. 1978. A model of the evolution of dioecy and gynodioecy. *American Naturalist* 112: 975–997.

CONNER, J., R. FRANKS, AND C. STEWART. 2003. Expression of additive genetic variances and covariances for wild radish floral traits: comparison between field and greenhouse environments. *Evolution* 57: 487–495.

CULLEY, T. M., A. DUNBAR-WALLIS, A. K. SAKAI, S. G. WELLER, M. MISHIO, D. R. CAMPBELL, AND M. HERZENACH. 2006. Genetic variation of ecophysiological traits in two gynodioecious species of *Schiedea* (Caryophyllaceae). *New Phytologist* 169: 589–601.

DELPH, L. F. 1996. Flower size dimorphism in plants with unisexual flowers. *In* D. G. Lloyd and S. C. H. Barrett [eds.], Floral biology: studies on floral evolution in animal-pollinated plants, 217–237. Chapman and Hall, New York, New York, USA.

DELPH, L. F. 2005. Processes that constrain and facilitate the evolution of sexual dimorphism. *American Naturalist* (Supplement) 166: S1–S4.

DIGGLE, P. K. 1995. Architectural effects and the interpretation of patterns of fruit and seed development. *Annual Review of Ecology and Systematics* 26: 531–552.

DONOHUE, K., E. H. PYLE, D. MESSIQUA, M. S. HESCHEL, AND J. SCHMITT. 2000. Density dependence and population differentiation of genetic architecture in *Impatiens capensis* in natural environments. *Evolution* 54: 1969–1981.

FALCONER, D. S., AND T. F. C. MACKAY. 1996. Introduction to quantitative genetics. Prentice Hall, New York, New York, USA.

FRIEDMAN, J., AND L. D. HARDER. 2004. Inflorescence architecture and wind pollination in six grass species. *Functional Ecology* 18: 851–860.

FRIEDMAN, J., AND L. D. HARDER. 2005. Functional associations of floret and inflorescence traits among grass species. *American Journal of Botany* 92: 1862–1870.

GEBER, M. A., T. E. DAWSON, AND L. F. DELPH. 1999. Gender and sexual dimorphism in flowering plants. Springer-Verlag, Heidelberg, Germany.

GOLONKA, A., A. K. SAKAI, AND S. G. WELLER. 2005. Evolution of wind pollination and sexual dimorphism: phenotypic changes in floral traits of *Schiedea* (Caryophyllaceae). *American Journal of Botany* 92: 1492–1502.

HOLLAND, J. B., W. E. NYQUIST, AND C. T. CERVANTES-MARTÍNEZ. 2003. Estimating and interpreting heritability for plant breeding: an update. *Plant Breeding Reviews* 22: 9–112.

HOULE, D., J. MEZEY, AND P. GALPERN. 2002. Interpretation of the results of common principal components analyses. *Evolution* 56: 433–440.

JANZEN, D. H. 1989. Natural history of a wind-pollinated Central American legume tree (*Ateleia Herbert-smithii*). *In* C. C. Stirton and J. Zarucchi [eds.], Advances in legume systematics, vol. 2, 733–769. Royal Botanical Gardens, Kew, UK.

KEARSEY, M. J. 1965. Biometrical analysis of a random mating population: a comparison of five experimental designs. *Heredity* 20: 205–235.

KIRCHER, P. 1986. Untersuchungen zur Blüten- un Infloreszenzmorphologie, Embryologie und Systematik der Restionaceen im Vergleich mit Gramineen und verwandten Familien. Dissertationes Botanicae, Band 94. J. Cramer, Berlin, Germany.

LANDE, R. 1979. Quantitative genetic analysis of multivariate evolution applied to brain: body size allometry. *Evolution* 33: 402–416.

LANDE, R. 1988. Genetics and demography in biological conservation. *Science* 241: 1455–1460.

LANDE, R., AND S. J. ARNOLD. 1983. The measurement of selection on correlated characters. *Evolution* 37: 1210–1226.

LITTELL, R. C., G. A. MILLIKEN, W. W. STROUP, AND R. D. WOLFINGER. 1996. SAS system for mixed models. SAS Institute, Cary, North Carolina, USA.

LLOYD, D. G., AND C. J. WEBB. 1977. Secondary sex characteristics of plants. *Botanical Review* 43: 177–216.

LLOYD, D. G., AND C. J. WEBB. 1986. The avoidance of interference between the presentation of pollen and stigmas in angiosperms I. Dichogamy. *New Zealand Journal of Botany* 24: 135–162.

LYNCH, M., AND B. WALSH. 1998. Genetics and analysis of quantitative traits. Sinauer, Sunderland, Massachusetts, USA.

MEAGHER, T. R. 1992. The quantitative genetics of sexual dimorphism in *Silene latifolia* (Caryophyllaceae). I. Genetic variation. *Evolution* 46: 445–457.

MEZEY, J. G., AND D. HOULE. 2003. Comparing G matrices: are common principal components informative? *Genetics* 165: 411–425.

MORAN, M. D. 2003. Arguments for rejecting the sequential Bonferroni in ecological studies. *Oikos* 100: 403–405.

NEPOKROEFF, M., W. L. WAGNER, P. S. SOLTIS, S. G. WELLER, D. E. SOLTIS, A. K. SAKAI, AND E. A. ZIMMER. 2005. Phylogeny. *In* W. L. Wagner, S. G. Weller, and A. K. Sakai [eds.], Monograph of Schiedea (Caryophyllaceae-Alsinoideae). *Systematic Botany Monographs* 72: 13–20, plate 2.

PHILLIPS, P. C. 1998. CPC: common principal component analysis program. University of Oregon. Website http://darkwing.uoregon.edu/~pphil/software.html [accessed 21 February 2007].

PHILLIPS, P. C., AND S. J. ARNOLD. 1999. Hierarchical comparison of genetic variance-covariance matrices. I. Using the Flury analysis. *Evolution* 53: 1506–1515.

PROCTOR, M., P. YEO, AND A. LACK. 1996. The pollination of flowers. Taplinger Publishing, New York, New York, USA.

QUINN, J. A. 1991. Evolution of dioecy in *Buchloe dactyloides* (Gramineae): tests for sex-specific vegetative characters, ecological differences, and sexual niche-partitioning. *American Journal of Botany* 78: 481–488.

ROFF, D. A., AND T. A. MOUSSEAU. 1999. Does natural selection alter genetic architecture? An evaluation of quantitative genetic variation among populations of *Allonemobius socius* and *A. fasciatus*. *Journal of Evolutionary Biology* 12: 361–369.

SAKAI, A. K., S. G. WELLER, M.-L. CHEN, S.-Y. CHOU, AND C. TASANONT. 1997. Evolution of gynodioecy and maintenance of females: the role of inbreeding depression, outcrossing rates, and resource allocation in *Schiedea adamantis* (Caryophyllaceae). *Evolution* 51: 724–736.

SAKAI, A. K., S. G. WELLER, T. M. CULLEY, D. R. CAMPBELL, A. K. DUNBAR-WALLIS, AND A. ANDRES. In press. Sexual dimorphism and the genetic potential for evolution of sex allocation in the gynodioecious plant, *Schiedea salicaria*. *Journal of Evolutionary Biology*.

SAS INSTITUTE. 2002–2003. SAS, version 9.1. SAS Institute, Cary, North Carolina, USA.

SEARLE, S. R., G. CASELLA, AND C. E. MCCULLOCH. 1992. Variance components. John Wiley, New York, New York, USA.

SHAW, R. G. 1987. Maximum-likelihood approaches applied to quantitative genetics of natural populations. *Evolution* 41: 812–826.

SOKAL, R. R., AND F. J. ROHLF. 1995. Biometry. W. H. Freeman, New York, New York, USA.

STEPPAN, S. J., P. C. PHILLIPS, AND D. HOULE. 2002. Comparative quantitative genetics: evolution of the G matrix. *Trends in Ecology and Evolution* 17: 320–327.

VERHOEVEN, K. J. F., K. L. SIMONSEN, AND L. M. MCINTYRE. 2005. Implementing false discovery rate control: increasing your power. *Oikos* 108: 643–647.

WAGNER, W. L., S. G. WELLER, AND A. K. SAKAI. 2005. Monograph of *Schiedea* (Caryophyllaceae-Alsinoideae). *Systematic Botany Monographs* 72: 1–169.

WALDMANN, P., AND S. ANDERSSON. 2000. Comparison of genetic (co)variance matrices within and between *Scabiosa canescens* and *S. columbaria*. *Journal of Evolutionary Biology* 13: 826–835.

WELLER, S. G., AND A. K. SAKAI. 1991. The genetic basis of male sterility in *Schiedea* (Caryophyllaceae), an endemic Hawaiian genus. *Heredity* 67: 265–273.

WELLER, S. G., AND A. K. SAKAI. 2005. Selfing and resource allocation in *Schiedea salicaria* (Caryophyllaceae), a gynodioecious species. *Journal of Evolutionary Biology* 18: 301–308.

WELLER, S. G., A. K. SAKAI, D. R. CAMPBELL, T. M. CULLEY, AND A. K. DUNBAR-WALLIS. 2006. Predicting the pathway to wind pollination: heritabilities and genetic correlations of inflorescence traits associated with wind pollination in *Schiedea salicaria* (Caryophyllaceae). *Journal of Evolutionary Biology* 19: 331–342.

WELLER, S. G., A. K. SAKAI, A. E. RANKIN, A. GOLONKA, B. KUTCHER, AND K. ASHBY. 1998. Dioecy and the evolution of pollination systems in *Schiedea* and *Alsinidendron* (Caryophyllaceae: Alsinoideae) in the Hawaiian Islands. *American Journal of Botany* 85: 1377–1388.

WELLER, S. G., A. K. SAKAI, AND C. STRAUB. 1996. Allozyme diversity and genetic identity in *Schiedea* and *Alsinidendron* (Caryophyllaceae: Alsinoideae) in Hawai'i. *Evolution* 50: 23–34.

WIDÉN, B., S. ANDERSSON, G.-Y. RAO, AND M. WIDÉN. 2002. Population divergence of genetic (co)variance matrices in a subdivided plant species, *Brassica cretica*. *Journal of Evolutionary Biology* 15: 961–970.