

Genetic variation of ecophysiological traits in two gynodioecious species of *Schiedea* (Caryophyllaceae)

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Summary

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- Evolution of dimorphic breeding systems may involve changes in ecophysiological traits as well as floral morphology because of greater resource demands on females. Differences between related species suggest that ecophysiological traits should be heritable, and species with higher female frequencies should show greater sexual differentiation.
- We used modified partial diallel crossing designs to estimate narrow-sense heritabilities and genetic correlations of sex-specific ecophysiological and morphological traits in closely related gynodioecious *Schiedea salicaria* (13% females) and *Schiedea adamantis* (39% females).
- In *S. salicaria*, hermaphrodites and females differed in photosynthetic rate and specific leaf area (SLA). Narrow-sense heritabilities were significant for stomatal conductance, SLA and inflorescence number in hermaphrodites, and for SLA and inflorescence number in females. *Schiedea adamantis* had no sexual dimorphism in measured traits; stomatal conductance, stem number and inflorescence number were heritable in females, and stem number was heritable in hermaphrodites. In both species, significant genetic correlations of traits between sexes were rare, indicating that traits can evolve independently in response to sex-differential selection. Significant genetic correlations were detected between certain traits within sexes of both species.
- Low heritability of some ecophysiological traits may reflect low additive genetic variability or high phenotypic plasticity in these traits.

Key words: breeding systems, Caryophyllaceae, ecophysiology, gynodioecy, quantitative genetics, resource acquisition, *Schiedea*, sexual dimorphism.

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Introduction

Although most flowering plants are hermaphroditic, evolution of separate sexes has evolved independently several times, presumably as a mechanism to promote outcrossing and avoid the deleterious consequences of inbreeding depression. With nuclear inheritance of sex expression, one common pathway to dioecy (separate unisexual male and female plants) is through gynodioecy, a breeding system with females and hermaphrodites

in populations (Darwin, 1877; Lewis, 1942; Lloyd, 1976, 1980; Charlesworth & Charlesworth, 1978, 1979; Bawa, 1980; Schultz, 1999). Once females are present in a population, selection may favor greater male function in hermaphrodites (Charlesworth & Charlesworth, 1978, 1989, 1999; Charnov, 1982; Charlesworth & Guttman, 1999). These changes in breeding system involve modifications in morphological traits associated with reproduction, but changes in physiological traits may also occur with the evolution of separate sexes if

these traits are heritable and if selective forces differ for females and hermaphrodites.

Selection pressures on females and hermaphrodites may diverge because of the larger resource investment in reproduction by females in many dimorphic species (Delph, 1999), leading to sex-specific differences in physiological traits, flower size, and other morphological traits (Dawson & Geber, 1999). Relatively few studies have examined sexual dimorphism in physiological traits (Dawson & Geber, 1999) or the genetic potential for changes in physiological traits with the evolution of dimorphic breeding systems (Geber & Dawson, 1997; Arntz & Delph, 2001), which are often associated with shifts in habitat (Weller *et al.*, 1990, 1998; Barrett, 1992; Case & Barrett, 2001, 2004). Increased gender differentiation has been observed in drier sites, in comparison with hermaphroditism or monoecy that typically occurs in wetter habitats (Costich, 1995; Sakai & Weller, 1999).

Studies of gynodioecious species have revealed only a few significant differences in ecophysiological traits between the sexes (Poot *et al.*, 1996; Dawson & Geber, 1999; Caruso *et al.*, 2003; Schultz, 2003). For example, females had significantly higher photosynthetic rates than hermaphrodites in *Lobelia siphilitica* (Caruso *et al.*, 2003), but not in *Sidalcea hirtipes* (Schultz, 2003) or *Plantago lanceolata* (Poot *et al.*, 1996). In the more frequently examined dioecious species, the mean photosynthetic rate of females relative to males has been higher (Dawson & Ehleringer, 1993; Obeso *et al.*, 1998); lower (Dawson & Bliss, 1993; Marshall *et al.*, 1993; Gehring & Monson, 1994; Laporte & Delph, 1996); or similar (Hogan *et al.*, 1998; Wang & Griffin, 2003).

The response of plants to selection on ecophysiological traits and the evolution of sexual dimorphism in these traits will depend on both the strength of selection and trait heritability. Despite the potential adaptive significance of ecophysiological traits, few studies have examined their heritability (reviewed by Ackerly *et al.*, 2000; Arntz & Delph, 2001; Geber & Griffin, 2003), especially in comparison with the many other investigations of morphological traits (Elle, 1998; Ashman, 1999, 2003; Mazer *et al.*, 1999; Meagher, 1999; Hansen *et al.*, 2003; Caruso, 2004). In general, ecophysiological estimates have been based on broad-sense heritabilities that include not only narrow-sense heritabilities but also maternal effects (Scheiner *et al.*, 1984; Schuster *et al.*, 1992; Donovan & Ehleringer, 1994; Dudley, 1996; Geber & Dawson, 1997; Johnsen *et al.*, 1999), and these measurements have exhibited a broad range of values (e.g. 0.10–0.87 for *A*, the photosynthetic rate; Scheiner *et al.*, 1984; Dudley, 1996; Geber & Dawson, 1997). In studies of narrow-sense heritabilities for gynodioecious species, Tonsor & Goodnight (1997) detected a heritability of 0.05 in *A* in *P. lanceolata* and Caruso *et al.* (2005) reported a heritability of 0.43 for the same trait in *L. siphilitica*.

Genetic correlations of ecophysiological traits will also influence how rapidly these traits will evolve in concert with sexual dimorphism. Strong positive genetic correlations between

homologous traits in two sexes (e.g. photosynthetic rate in females and hermaphrodites) make it more difficult for these traits to evolve independently in response to sex-differential selection. In contrast, traits are more likely to evolve independently in the sexes if these correlations are absent. Genetic correlations between the sexes may be especially influential in populations where gynodioecy is recent and females are rare (Eckhart, 1999). In addition, genetic correlations between different traits within a sex will influence how tightly those traits evolve in concert with one another.

The Hawaiian endemic genus *Schiedea* is well suited to ecophysiological investigations of dimorphic taxa because this monophyletic group contains species with a diversity of breeding systems (Weller & Sakai, 1992; Wagner *et al.*, 1995; Sakai *et al.*, 1997a; Weller *et al.*, 1998; Wagner *et al.*, 2005). Unlike many gynodioecious species with nuclear-cytoplasmic inheritance of male sterility, male sterility in *Schiedea* is determined by a single nuclear gene (Weller & Sakai, 1991). Females are homozygous recessive (*hh*) and hermaphrodites are either heterozygous (*Hh*) or homozygous dominant (*HH*). Hermaphroditism is the ancestral condition for the genus, and most of the 24 hermaphroditic species occur in wet or mesic areas (Nepokroeff *et al.*, 2005; Wagner *et al.*, 2005). With nuclear control of male sterility and with selection for separate sexes in dry habitats (Weller & Sakai, 1990), several subdioecious and dioecious species have evolved within *Schiedea*. All 10 dimorphic (gynodioecious, subdioecious, and dioecious) species occur in dry habitats, where water is a limiting resource (Weller & Sakai, 1990).

We focused on two closely related gynodioecious species that vary in frequency of females, *Schiedea salicaria* with a low frequency of females (13%) and *Schiedea adamantis* with a higher frequency of females (39%) and greater seed production of females than hermaphrodites (Sakai *et al.*, 1989; Weller *et al.*, 1990; Sakai *et al.*, 1997b). High levels of inbreeding depression and selfing in both species indicate that higher frequencies of females are favored (Sakai *et al.*, 1989; Sakai *et al.*, 1997b; Weller & Sakai, 2005). These results suggest that these two *Schiedea* species are at different stages in the evolution of gynodioecy, in contrast to other genera with nuclear-cytoplasmic male sterility in which gynodioecy may be evolutionary stable (Webb, 1999; Charlesworth, 2002).

Females of these two species may be under stronger selection to maintain or increase carbon assimilation, relative to hermaphrodites. In *S. adamantis* females produce 2.3 times more seeds than hermaphrodites (Sakai *et al.*, 1997b); consequently, reproductive costs of females of *S. adamantis* may be higher than those of *S. salicaria* where seed production of females and hermaphrodites is similar (Weller & Sakai, 2005). The dry habitats of these two species may exert stronger selection on females to maintain carbon gain despite water stress, which can lead to changes in photosynthetic physiology as well as alterations in hydraulic characteristics, root growth and vegetative morphology. For example, increased stomatal opening

in females may increase acquisition of CO₂ necessary to offset high reproductive costs, but this also allows water to diffuse out rapidly, potentially decreasing water-use efficiency (WUE) (Dawson & Geber, 1999). In addition to higher carbon-assimilation rates (hereafter referred to as photosynthetic rates), greater carbon uptake in females can also occur through the production of more photosynthetic tissue, increased specific leaf area (SLA) and/or changes in biochemical pathways (Delph & Meagher, 1995; Geber & Dawson, 1997; Caruso *et al.*, 2003).

We examined the extent of sexual dimorphism, the amount of heritable genetic variation, and genetic correlations among ecophysiological traits within *S. salicaria* and *S. adamantis*. Instantaneous photosynthetic rate (A_{area}), stomatal conductance to water vapor (g_s), and an estimate of instantaneous WUE (A/E , where E is the transpiration rate) were measured because they are critical in carbon assimilation and water balance, both integral components of adaptation to dry habitats. We also measured SLA (leaf area/leaf mass), a key factor in both light interception and carbon gain, which can influence the relative growth rate. Because we found some sexual dimorphism in SLA, we measured photosynthetic rate expressed on both a per area basis (A_{area}) as well as a per unit mass basis (A_{mass}). Number of stems was used as an estimate of plant size, and number of inflorescences was used as an index of reproduction. We asked the following questions for each species: (1) Do females and hermaphrodites differ in ecophysiological traits? (2) Is there significant narrow-sense heritability in ecophysiological traits? (3) Are these traits genetically correlated with one another? (4) How will genetic correlations affect the evolution of sexual dimorphism in these traits? We predicted that females and hermaphrodites would differ in ecophysiological traits and in size, but more so in *S. adamantis* because of its higher frequency of females and greater difference in seed production between females and hermaphrodites. These traits were expected to show narrow-sense heritability, given changes in breeding system and habitat that have occurred in closely related species, and assuming that strong selection has not depleted genetic variation for these traits. We also predicted that genetic correlations would be consistent with adaptations to dry habitats, although positive genetic correlations between the sexes in homologous traits might constrain rapid evolution of sexual dimorphism.

Materials and Methods

Study organisms and crossing design

Both *Schiedea salicaria* Hillebr. and *Schiedea adamantis* St. John are perennial woody shrubs endemic to the Hawaiian Islands. *Schiedea salicaria* occurs in several populations, but is limited to remnant dry shrubland in the West Maui Mountains at approx. 180–360 m elevation. *Schiedea adamantis* is found at a single site on the slope of Diamond Head Crater (O'ahu)

at approx. 125 m (Wagner *et al.*, 1990). There is no apparent spatial segregation of the sexes within either of the two populations studied (A.K.S. and S.G.W., personal observation), in contrast to subdioecious *Schiedea globosa* (Sakai & Weller, 1991). Both species are wind-pollinated (Weller *et al.*, 1998), and grow, flower and fruit during the wetter winter months. During the dry summers, plants are deciduous and dormant. In *S. adamantis*, a severe drought from 1998 to 2002 eliminated all but two individuals in the population.

Plants of both species used in this experiment originated as field seeds or cuttings and were grown in the glasshouse at the University of California, Irvine in 1999 (*S. salicaria*) and 2001 (*S. adamantis* – using samples collected before the population decline) as part of larger studies of quantitative genetics and artificial selection of sex allocation traits. For *S. salicaria*, parental plants consisted of 35 unrelated hermaphrodites (sires) that were heterozygous for the sex gene, and 35 females (dams) that were each related to one of the hermaphrodites as either full or half-sibs. One hermaphrodite and one female were chosen randomly from each of the 35 sibships. Using a modified partial diallel crossing design for each species, each hermaphrodite was crossed with three unrelated females, and each female was crossed with three unrelated hermaphrodites, following Meagher (1992). A few crosses failed to produce enough progeny, resulting in 91 instead of 105 full sibships in 35 paternal half-sib families of *S. salicaria*. The crossing design for *S. adamantis* was identical, except that 30 heterozygous hermaphrodites were used as sires (each crossed to three unrelated females), resulting in 90 full sibships in 30 paternal half-sib families.

Seeds of *S. salicaria* were planted in spring 2000, and the sex of each individual was determined when the plant flowered. Five female and five hermaphroditic individuals per full sibship were selected randomly, and in August 2000 all plants were transferred from 5-cm to 8-cm pots. Seeds of *S. adamantis* were planted in spring 2002 and treated in the same manner as *S. salicaria*, and plants were transplanted in August 2002. For individuals of both species, Grow More fertilizer (20–20–20) was applied weekly throughout the experiment and plants were watered as needed.

Physiological measurements

Schiedea salicaria During the period 7–14 September 2001, 599 progeny (296 females and 303 hermaphrodites) representing all 91 full sibship families were lightly pruned and transplanted from 500-ml to 2.6-l pots with UC soil-less adult mix. Plants were placed in flats (five plants per flat) that were randomized with respect to bench location every few days. Twenty-four h before any physiological measures, plants to be measured were randomly selected with respect to sex and family, but with the requirement that they had at least one inflorescence. These plants were watered and evenly spaced on glasshouse benches to maximize light availability. The numbers

of stems and inflorescences on each plant were recorded as an estimate of plant size and reproduction at the time of physiological measurements.

In September 2001, light-response curves were generated in the glasshouse from 10 randomly selected plants to determine the optimal photosynthetically active radiation (PAR). All measurements were taken with an infrared gas analyzer (LI-6400, Li-Cor, Lincoln, NE, USA) using unshaded leaves at the second node below a newly flowering inflorescence. CO₂ concentration (370 µl l⁻¹) and leaf temperature (26°C) were kept constant within the cuvette, and all measurements were taken between 09:00 and 14:00 h Pacific Standard Time. The photosynthetic rate (A) was first obtained at 1200 µmol m⁻² s⁻¹ and then downward at every 200 µmol m⁻² s⁻¹ interval until reaching 0 µmol m⁻² s⁻¹. For *S. salicaria*, the light-response curve indicated that a PAR of 800 µmol m⁻² s⁻¹ would be appropriate for measuring the maximum light-saturated photosynthetic rate (A_{\max}) on a leaf-area basis. Leaves typically took approx. 5 min to reach equilibrium following exposure to saturating light conditions. Several plants measured at three different times throughout the day exhibited little variation in trait values.

Ecophysiological traits were measured between October and November 2001. A single, unshaded leaf at the second node below a newly flowering inflorescence was measured on each plant. The LI-6400 was used to quantify the instantaneous photosynthetic rate (A), stomatal conductance to water vapor (g_s), and an estimate of instantaneous WUE (A/E), adjusting for the leaf area within the cuvette. CO₂ concentration (370 µl l⁻¹), flow rate (350 µmol s⁻¹), PAR (800 µmol m⁻² s⁻¹), leaf temperature (26°C), and relative humidity (40–60%) were held constant. Each leaf sample was then dried for at least 24 h at 60°C and weighed to the nearest µg, and SLA was calculated as (leaf area/leaf mass). The photosynthetic rate was also expressed on a per unit mass basis (A_{mass}) for each individual by multiplying the original area-based estimate of A (hereafter referred to as A_{area}) by SLA. Mass- and area-based estimates of A may vary partly because of differences in the thickness and density of a leaf, which influences the number of chlorophyll units. The remaining leaf on the second node, as well as the two pairs of leaves on the first and third nodes, were collected for ¹³C stable isotope analysis, a method for measuring integrated WUE over the lifetime of the leaf (Farquhar *et al.*, 1982). These leaves were stored in glassine envelopes, dried at 60°C for 24 h, and ground using a Wig-L-Bug (Bratt Technologies Inc., East Orange, NJ, USA).

A preliminary carbon isotope analysis was conducted with plants from the 10 full-sib crosses (five to nine plants per cross) with the highest (15.6–17.6 µmol m⁻² s⁻¹; $N = 75$) and lowest (9.2–12.1 µmol m⁻² s⁻¹; $N = 70$) area-based photosynthetic rates (145 plants). A_{area} was used instead of A/E as a predictor of variation in carbon isotope values because A_{area} exhibited the greatest variation among crosses and had the highest heritability in a preliminary analysis. Leaf samples of plants

from these 20 crosses were sent to the University of California, Berkeley stable isotope laboratory for analysis of leaf nitrogen content and carbon isotope ratio ($\delta^{13}\text{C}$). No significant differences were detected between mean values of $\delta^{13}\text{C}$ in high and low crosses (t -test: $t = 1.510$, $df = 18.0$, $P = 0.148$). Furthermore, no significant differences were detected between sexes (paired t -test: $t = 1.64$, $df = 19$, $P = 0.116$), nor between high and low crosses when analyzed within females (t -test: $t = 1.17$, $df = 18.0$, $P = 0.257$) or hermaphrodites (t -test: $t = 0.876$, $df = 18.0$, $P = 0.393$). As a consequence, $\delta^{13}\text{C}$ values were not examined in the larger sample of plants.

Schiedea adamantis All plants were treated in the same manner as *S. salicaria* with respect to pruning, transplanting, bench randomization and watering 24 h before measurement. We excluded two full sib-ships because of the poor health of some plants, resulting in 422 plants of *S. adamantis* (214 females and 208 hermaphrodites) representing 88 of the 90 crosses. Based on light-response curves generated in the glasshouse during summer 2003, a PAR of 1200 µmol m⁻² s⁻¹ was used for *S. adamantis*. All measurements were taken with the LI-6400 with a constant CO₂ concentration (370 µl l⁻¹), leaf temperature (26°C) and relative humidity (40–60%). Ecophysiological (A_{area} , A_{mass} , g_s and WUE) and morphological traits (SLA, stem number and inflorescence number) of *S. adamantis* were measured in the glasshouse between August and November 2003.

Statistical analysis

Within each species, differences between female and hermaphrodite progeny were examined using paired t -tests on individual trait means of the 35 paternal half-sib families for *S. salicaria* and 30 paternal half-sib families for *S. adamantis*. Sexual dimorphism in ecophysiological traits was also investigated using MANOVA to account for multiple comparisons. In this analysis, WUE and A_{mass} were excluded because they were correlated with other traits already included (see below).

Narrow-sense heritability values (h^2) were estimated separately for hermaphrodite and female progeny for A_{area} , A_{mass} , g_s , WUE, SLA, and number of stems and inflorescences. Using SAS ver. 8.2 (SAS Institute, Cary, NC, USA), restricted maximum likelihood (REML; PROC MIXED) was used to estimate the variance caused by the random effects of paternal half-sibship (sire) and maternal half-sibship (dam) in each trait. This method is advantageous over least-squares means because of the unbalanced nature of the design. An interaction term (sire \times dam) was not included because missing cells in the design made interpretation of the interaction term difficult (Searle *et al.*, 1992) and interactions were not significant in preliminary analyses. Under this crossing design, additive genetic variance (V_A) is estimated by four times the variance caused by paternal half-sibship (Falconer & Mackay, 1996; Lynch & Walsh, 1998). Within each species, narrow-sense heritabilities were calculated

for each trait in each sex as the additive genetic variance (V_A) divided by the total variance (V_p). Significance of the paternal effect was assessed with a residual log likelihood-ratio test to compare the full model with a reduced model containing only the maternal effect and residual error (Littell *et al.*, 1996). A significant paternal effect suggests significant additive genetic variance, assuming no additive-additive epistasis (Lynch & Walsh, 1998). To determine if differences in h^2 between females and hermaphrodites within each species were caused by differences in additive genetic variance, the coefficient of additive genetic variation (CV_A) was calculated in each sex for each trait (Houle, 1992).

Because there was little sexual dimorphism in the traits measured (see below), we also combined the two sexes within each species for a larger sample size with greater statistical power ($N = 599$ plants in 35 paternal half-sibships for *S. salicaria*; $N = 422$ plants in 30 paternal half-sibships of *S. adamantis*). The ANOVA was similar to that conducted for the separate sexes, except that sex was included as a fixed factor, and sex \times maternal parent and sex \times paternal parent were considered random factors. The level of narrow-sense heritability was calculated as described previously.

To examine the combined effects of heritable variation and covariation of traits on the response to selection, we estimated the conditional heritability ($h^2_{(x|y)}$) for each trait in each sex of each species. Conditional heritability is the amount of heritable variation in each trait that is independent of both genetic correlations across sexes and the additive genetic variance in the other sex (Jensen *et al.*, 2003).

Genetic correlations between traits were estimated separately within females and hermaphrodites of each species, using best linear unbiased predictors (BLUPs) of sire breeding values obtained from PROC MIXED (SAS ver. 8.2; Conner *et al.*, 2003). Pearson correlation coefficients were then calculated between BLUPs of different traits within each sex of each species. Similarly, genetic correlations were also calculated

between BLUPs of females and hermaphrodites for homologous traits within each species. Significance levels were adjusted for multiple comparisons using the sequential Bonferroni method (Sokal & Rohlf, 1995). Only traits with nonzero narrow-sense heritabilities were used in the genetic correlations.

Results

Schiedea salicaria

Dimorphism Hermaphrodites had greater A_{mass} and SLA than females of *S. salicaria* (Table 1). There were no significant differences between the sexes in the instantaneous ecophysiological traits of A_{area} , g_s and WUE, or in the number of stems or inflorescences (Table 1). In a multivariate approach using A_{area} , g_s and SLA, significant differences were not detected between females and hermaphrodites (MANOVA; Wilk's lambda = 0.800, $F = 2.66$, $df = 3,32$, $P = 0.0647$).

Heritabilities Stomatal conductance (g_s) had significant heritable variation in hermaphrodites ($h^2 = 0.38$, $P = 0.005$) but not in females, and A_{area} showed a similar pattern, with heritable variation approaching significance in hermaphrodites ($h^2 = 0.25$, $P = 0.054$) but not in females (Table 2). SLA had heritable variation in both females ($h^2 = 0.49$) and hermaphrodites ($h^2 = 0.31$). Inflorescence number also had heritable variation in both sexes ($h^2 = 0.34$ in females, $h^2 = 0.28$ in hermaphrodites), but the number of stems did not exhibit significant heritability. There was no measurable heritable variation in either sex when photosynthetic rate was estimated on a mass basis (A_{mass}) because of low additive genetic variation. Instantaneous WUE also showed no significant heritable variation in either sex. The trend towards larger coefficients of additive genetic variation for A_{area} , g_s , WUE and SLA in hermaphrodites relative to females suggests that the higher heritabilities in hermaphrodites are associated with greater paternal variance

Table 1 Grand means of female and hermaphroditic progeny of 35 paternal families in *Schiedea salicaria* for the following ecophysiological and morphological traits: photosynthetic rate on an area basis (A_{area}) and a mass basis (A_{mass}), stomatal conductance to water vapor (g_s), instantaneous water-use efficiency (WUE, A/E), and specific leaf area (SLA). Differences between sexes for each trait were analyzed with a paired t -test

Trait	Females			Hermaphrodites			<i>P</i>
	Mean	SE	Range	Mean	SE	Range	
Ecophysiological							
A_{area} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	13.75	0.20	11.48–16.13	13.85	0.22	11.27–17.20	0.662
A_{mass} ($\mu\text{mol g}^{-1} \text{s}^{-1}$)	0.38	0.005	0.32–0.44	0.39	0.006	0.34–0.49	0.039
g_s ($\text{mmol m}^{-2} \text{s}^{-1}$)	0.21	0.005	0.14–0.26	0.21	0.006	0.14–0.31	0.992
WUE (mmol mol^{-1})	5.81	0.108	4.58–7.71	5.76	0.09	4.52–6.75	0.680
Morphological							
SLA ($\text{cm}^2 \text{mg}^{-1}$)	0.28	0.004	0.23–0.32	0.29	0.005	0.25–0.39	0.042
Stem number	4.84	0.18	2.75–7.22	4.94	0.23	2.50–8.78	0.664
Inflorescence number	7.37	0.30	4.92–12.58	6.88	0.30	3.75–10.00	0.203

Table 2 Narrow-sense heritabilities (h^2) of ecophysiological and morphological traits (see text for abbreviations) for female and hermaphroditic progeny of *Schiedea salicaria* based on 35 paternal families

Trait	Females					Hermaphrodites				
	h^2	χ^2	P	CV_A	$(b^2_{(x1,y)})$	h^2	χ^2	P	CV_A	$(b^2_{(x1,y)})$
Ecophysiological										
A_{area}	0	0	1	0	0	0.25	3.7	0.054	11.58	0
A_{mass}	0	0	1	0	0	0	0	1	0	0
g_s	0	0	1	0	0	0.38	7.7	0.005	26.23	0
WUE	0.09	0.3	0.584	7.70	0.05	0.13	1.0	0.317	8.91	0.07
Morphological										
SLA	0.49	9.3	0.002	11.33	0.45	0.31	5.6	0.018	15.03	0.28
Stem number	0.09	0.5	0.480	15.52	0.08	0.26	2.3	0.129	29.28	0.23
Inflorescence number	0.34	3.9	0.048	32.56	0.33	0.28	4.0	0.046	31.38	0.28

P values result from a residual log likelihood ratio test (χ^2); CV_A is the coefficient of additive genetic variation. Conditional heritability ($b^2_{(x1,y)}$) was also calculated for each trait in each sex as conditional on genetic values of the same trait in the other sex (Jensen *et al.*, 2003).

for these traits among the 35 half-sibships. Values for traits with significant heritability (h^2) were slightly reduced when the additive genetic variation in the opposite sex and genetic correlations across sex were accounted for ($b^2_{(x1,y)}$; Table 2).

When the two sexes were combined to maximize the statistical power in calculating the paternal variance component, substantial heritable variation in SLA was detected ($h^2 = 0.314$, $P = 0.008$), consistent with the results of individual sexes. Despite the larger sample sizes, narrow-sense heritabilities were low and nonsignificant for A_{area} ($h^2 = 0.09$, $P = 0.348$), A_{mass} ($h^2 = 0.02$, $P = 0.752$), g_s ($h^2 = 0.06$, $P = 0.554$), and WUE ($h^2 = 0.16$, $P = 0.069$). The interaction between sex and maternal or paternal parent was not significant for any of the ecophysiological traits.

Correlations Some pairs of traits with nonzero estimates of heritability had significant correlations (Table 3). In hermaphrodites, g_s was positively correlated with A_{area} ($r = 0.850$, $P < 0.0001$), and negatively correlated with WUE ($r = -0.820$,

$P < 0.0001$). In addition, A_{area} in hermaphrodites decreased with SLA ($r = -0.587$, $P = 0.0002$). Correlations of homologous ecophysiological traits between female and hermaphrodite siblings (Table 4) were significant for SLA ($r = 0.510$, $P = 0.0018$), a trait with significant narrow-sense heritabilities, and for WUE ($r = 0.365$, $P = 0.0312$), a trait with no significant heritability in either sex.

In hermaphrodites, the number of inflorescences was not correlated with any heritable trait measured (Table 3). By contrast, in females the number of inflorescences was positively correlated with the number of stems ($r = 0.530$, $P = 0.0011$). Both the number of inflorescences ($r = -0.337$, $P = 0.048$) and the number of stems ($r = -0.378$, $P = 0.025$) were negatively correlated with SLA (thicker or more dense leaves).

Schiedea adamantis

Dimorphism There were no significant differences between female and hermaphroditic progeny in any of the measured

Table 3 Estimates of genetic correlations for *Schiedea salicaria* within females (above diagonal) and hermaphrodites (below diagonal) of the following ecophysiological traits that exhibited nonzero heritability: photosynthetic rate on an area basis (A_{area}), stomatal conductance to water vapor (g_s), instantaneous water-use efficiency (WUE, A/E), and specific leaf area (SLA). Also included are the number of stems and inflorescences per plant

Trait	A_{area}	g_s	WUE	SLA	Stem number	Inflorescence number
A_{area}	–	n/a	n/a	n/a	n/a	n/a
g_s	0.850***	–	n/a	n/a	n/a	n/a
WUE	–0.559**	–0.820***	–	–0.194	0.237	0.049
SLA	–0.587**	–0.370	0.203	–	–0.378*	–0.337*
Stem number	0.049	–0.015	–0.007	–0.096	–	0.530*
Inflorescence number	0.100	0.101	0.007	0.159	0.191	–

Correlations that had traits with zero heritable variation in one sex are denoted n/a; A_{mass} was excluded because it exhibited zero heritable variation in both sexes.

$N = 35$ paternal half-sib families. P values were adjusted for multiple comparisons using the sequential Bonferroni method. *, $P < 0.05$; **, $P < 0.001$; ***, $P < 0.0001$.

Table 4 Estimates of genetic correlations between females and hermaphrodites for *Schiedea salicaria* and *S. adamantis* for the following homologous traits: photosynthetic rate on an area basis (A_{area}), stomatal conductance to water vapor (g_s), instantaneous water-use efficiency (WUE, A/E), specific leaf area (SLA), and the number of stems and inflorescences per plant

Trait	<i>S. salicaria</i>		<i>S. adamantis</i>	
	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
A_{area}	–	–	–	–
g_s	–	–	0.221	0.242
WUE	0.365	0.031*	–	–
SLA	0.510	0.0018*	–	–
Stem number	0.269	0.117	0.294	0.115
Inflorescence number	0.224	0.196	0.282	0.131

Correlation coefficients could not be calculated for some traits because of lack of variance among paternal families. Significant *P* values adjusted for multiple comparisons using the sequential Bonferroni method are indicated with an asterisk.

traits when compared individually (Table 5) or in a multivariate approach based on A_{area} , g_s and SLA (MANOVA; Wilk's lambda = 0.786, $F = 2.45$, $df = 3, 27$, $P = 0.0856$).

Heritabilities Significant heritable variation was detected in g_s in females ($h^2 = 0.39$), but not in hermaphrodites (Table 6). The number of stems exhibited significant heritable variation in both sexes ($h^2 = 0.47$ in females, 0.50 in hermaphrodites), while inflorescence number was only heritable in females ($h^2 = 0.46$). In contrast to *S. salicaria*, estimates of heritability and coefficients of additive genetic variance were generally higher in females than in hermaphrodites. Several values for narrow-sense heritability in ecophysiological traits of *S. adamantis* were very low because of low variation of the paternal variance component. In general, when heritability was adjusted to account for the additive genetic variation in the opposite sex and genetic correlations across sex ($h^2_{(x|y)}$), heritabilities of traits with low values dropped to zero, and heritabilities of traits with higher h^2 were slightly reduced (Table 6).

When the two sexes were combined in *S. adamantis*, g_s was heritable ($h^2 = 0.21$, $P = 0.003$), consistent with the previous

Table 5 Grand means of female and hermaphroditic progeny of 30 paternal families of *Schiedea adamantis* for ecophysiological and morphological traits (see text for abbreviations). Differences between sexes for each trait were analyzed with a paired *t*-test

Trait	Females			Hermaphrodites			<i>P</i>
	Mean	SE	Range	Mean	SE	Range	
Ecophysiological							
A_{area} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	13.89	0.22	12.11–17.08	13.65	0.17	11.85–16.18	0.356
A_{mass} ($\mu\text{mol g}^{-1} \text{s}^{-1}$)	0.42	0.01	0.33–0.51	0.42	0.01	0.33–0.52	0.709
g_s ($\text{mmol m}^{-2} \text{s}^{-1}$)	0.23	0.01	0.17–0.34	0.21	0.01	0.16–0.28	0.059
WUE (mmol mol^{-1})	4.97	0.13	3.70–6.42	5.11	0.12	4.12–6.12	0.395
Morphological							
SLA ($\text{cm}^2 \text{mg}^{-1}$)	0.31	0.004	0.26–0.37	0.31	0.005	0.26–0.38	0.121
Stem number	4.30	0.24	1.94–7.00	4.28	0.28	2.33–8.25	0.946
Inflorescence number	16.64	0.90	7.50–28.05	17.02	0.71	9.67–26.56	0.667

Table 6 Narrow-sense heritabilities (h^2) of female and hermaphroditic progeny of *Schiedea adamantis* from 30 paternal families for ecophysiological and morphological traits

Trait	Females					Hermaphrodites				
	h^2	χ^2	<i>P</i>	CV_A	$h^2_{(x y)}$	h^2	χ^2	<i>P</i>	CV_A	$h^2_{(x y)}$
Ecophysiological										
A_{area}	0.24	1.7	0.192	8.79	0	0	0	1	0	0
A_{mass}	0.20	1.2	0.273	9.62	0	0	0	1	0	0
g_s	0.39	4.8	0.028	23.75	0.38	0.20	1.2	0.273	15.4	0.20
WUE	0.04	0.1	0.752	1.44	0	0	0	1	0	0
Morphological										
SLA	0	0	1	0	0	0.21	1.3	0.254	8.6	0
Stem number	0.47	6.3	0.012	39.46	0.43	0.50	5.5	0.019	46.8	0.46
Inflorescence number	0.46	6.1	0.014	37.91	0.41	0.21	1.6	0.206	23.0	0.19

P values result from a residual log-likelihood ratio test (χ^2); CV_A is the coefficient of additive genetic variation. Conditional heritability ($h^2_{(x|y)}$) was also calculated for each trait in each sex as conditional on genetic values of the same trait in the other sex (Jensen *et al.*, 2003).

Table 7 Estimates of genetic correlations for *Schiedea adamantis* within females (above diagonal) and hermaphrodites (below diagonal) of the following ecophysiological traits that exhibited nonzero heritability: photosynthetic rate on an area basis (A_{area}) and a mass basis (A_{mass}), stomatal conductance to water vapor (g_s), instantaneous water-use efficiency (WUE, A/E), and specific leaf area (SLA). Also included are the number of stems and inflorescences per plant

Trait	A_{area}	A_{mass}	g_s	WUE	SLA	Stem number	Inflorescence number
A_{area}	–	0.726***	0.560**	0.003	n/a	0.207	0.293
A_{mass}	n/a	–	0.271	0.108	n/a	–0.091	–0.007
g_s	n/a	n/a	–	–0.679***	n/a	0.219	0.453*
WUE	n/a	n/a	n/a	–	n/a	–0.032	–0.341
SLA	n/a	n/a	0.023	n/a	–	n/a	n/a
Stem number	n/a	n/a	–0.062	n/a	–0.252	–	0.394*
Inflorescence number	n/a	n/a	0.044	n/a	–0.117	0.254	–

Correlations that involve traits that show zero heritable variation are denoted as n/a; $N = 30$ paternal half-sib families. P values were adjusted for multiple comparisons using the sequential Bonferroni method. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

analysis for females of *S. adamantis*. Narrow-sense heritabilities remained low and nonsignificant for A_{area} ($h^2 = 0.28$, $P = 0.752$), A_{mass} ($h^2 = 0.12$, $P = 0.273$), WUE ($h^2 = 0.04$, $P = 0.584$), and SLA ($h^2 = 0.08$, $P = 0.406$).

Correlations Some traits with nonzero heritability estimates were genetically correlated with one another within females of *S. adamantis* (Table 7). Stomatal conductance (g_s) was positively correlated with A_{area} ($r = 0.560$, $P = 0.0013$), negatively correlated with WUE ($r = -0.679$, $P < 0.0001$), and positively correlated with inflorescence number ($r = 0.453$, $P = 0.012$). As in *S. salicaria*, female *S. adamantis* plants with a larger number of stems also had more inflorescences ($r = 0.394$, $P = 0.031$). By contrast, in hermaphrodites there were no significant correlations among the four traits with nonzero estimates of heritability (g_s , SLA, stem number and inflorescence number). There were no significant genetic correlations of homologous traits between female and hermaphrodite siblings of *S. adamantis* (Table 4).

Discussion

We found significant heritability for some ecophysiological traits in certain sexes of *S. salicaria* and *S. adamantis*, suggesting that natural selection could modify these physiological traits as species colonize new environments. Phylogenetic analysis of *Schiedea* indicates that the evolution of dimorphic breeding systems in gynodioecious species is associated with shifts into arid, high-light habitats (Weller *et al.*, 1990; Sakai *et al.*, 1995; Sakai & Weller, 1999; Nepokroeff *et al.*, 2005). This shift in habitat, as well as the greater resource demands on females with greater fruit production, suggests selection should occur on ecophysiological as well as morphological traits. In these dry environments, increased carbon assimilation at the expense of water loss may be particularly important to offset the higher reproductive costs of females. Physiological differences occur between closely related species in the field (T.E. Dawson and co-workers, unpublished data) and in a common environment (M.M., A.K.S. and S.G.W., unpublished data),

indicating that a response to selection on physiological traits in different environments has occurred. Consequently, we predicted that ecophysiological traits should be heritable, especially in *S. adamantis*, which has a higher frequency of females than *S. salicaria*, a species that is more similar to hermaphroditic species in floral traits (Golonka *et al.*, 2005). We also predicted that *S. adamantis* would show greater sexual dimorphism in ecophysiological traits. Contrary to our predictions, sexual dimorphism occurred in only two traits of *S. salicaria* and was absent in *S. adamantis*. We found narrow-sense heritabilities for several ecophysiological traits, although their significance varied by both sex and species, and not necessarily in the directions predicted. In several cases, heritabilities may be limited by low levels of variation in traits, or phenotypic plasticity associated with differences in the immediate environment of the leaf may mask more subtle genetic differences. The effects of genetic correlations among traits were limited by the number of traits with significant heritabilities.

Sexual dimorphism In *S. salicaria* we found evidence for sexual dimorphism in two traits, A_{mass} and SLA, although in the opposite direction to that predicted if females have higher reproductive costs. Females had thicker and/or denser leaves (lower SLA), which could potentially slow their growth rate (Lambers *et al.*, 1998). Lower SLA was accompanied by lower mass-based photosynthetic rates (A_{mass}) in females, although area-based photosynthetic rates were similar for the sexes. Carbon assimilation of the two sexes could differ if the sexes vary in the size or number of leaves produced, or in lifespan. Individuals did not differ visibly in size by sex (T.M.C., personal observation) or in the numbers of stems or inflorescences produced, but our measures of above-ground biomass were limited because these plants were part of an artificial selection experiment and could not be harvested. *Schiedea salicaria* is apparently in the early stages of the evolution of dimorphism, so the lack of sexual dimorphism in most ecophysiological traits is not surprising given the absence of differentiation of females and hermaphrodites in other morphological traits.

We expected to see greater differentiation between the sexes in ecophysiological traits of *S. adamantis* than in *S. salicaria*, because *S. adamantis* has a much higher percentage of females that produce far more seeds than hermaphrodites (Sakai *et al.*, 1997b). None of the traits measured in *S. adamantis* showed sexual dimorphism, and field comparisons of ecophysiological traits in *S. salicaria* and *S. adamantis* also failed to detect sex differences in A_{area} , g_s and A/E (T.E. Dawson and co-workers, unpublished data). The absence of sex differences in many traits of *S. adamantis* and *S. salicaria* may also reflect the phenological stage of our measurements, taken when inflorescences were beginning to flower. Differences between sexes in traits such as A may only be evident with greater reproductive demand that occurs at the end of flowering and/or as fruits are forming (Seger & Eckhart, 1996), as in *Silene latifolia* (Dawson & Geber, 1999).

The few other studies comparing ecophysiological traits in separate sexes of gynodioecious species have generally yielded mixed results. As in *S. adamantis*, there were no significant sex differences in A_{area} for *S. hirtipes* (Schultz, 2003) or A_{mass} in *P. lanceolata* grown under optimal conditions (Poot *et al.*, 1996). In contrast, sex differences were evident in both *S. salicaria* and *L. siphilitica* but the direction of the difference varied; hermaphrodites of *S. salicaria* exhibited higher values of A_{mass} than females, but prereproductive females of *L. siphilitica* had greater A_{mass} than hermaphrodites (Caruso *et al.*, 2003). WUE did not differ between the sexes of *Schiedea* or other gynodioecious species, except in *P. lanceolata* where female lines exhibited greater WUE (Poot *et al.*, 1996). SLA was typically similar between the sexes in most gynodioecious species, but did differ in both *S. salicaria* and *P. lanceolata* (Schultz, 2003). Like *L. siphilitica*, females of *S. adamantis* had significantly higher g_s , but *S. salicaria* was more similar to *S. hirtipes* and *P. lanceolata* in which no sex differences were evident in g_s (Poot *et al.*, 1996; Schultz, 2003). Although physiological traits dependent on nutrient uptake may also differ between sexes (Eckhart & Chapin, 1997), this was not detected in females and hermaphrodites of *P. lanceolata* from different nitrogen conditions (Poot *et al.*, 1996). In *S. salicaria* and *S. adamantis*, nutrient availability probably affects ecophysiological traits (as detected in hermaphroditic *Schiedea lydgatei*; Norman *et al.*, 1995), but sex differences in nutrient uptake and use have not yet been examined.

Narrow-sense heritabilities of traits and genetic correlations within sexes In *S. salicaria*, hermaphrodites had significant or marginally significant heritabilities for A_{area} , g_s and SLA, while females exhibited detectable heritability for SLA. Genetic correlations between these traits may be most important in hermaphrodites of *S. salicaria*, where three traits had detectable heritability and a significant within-sex correlation. A_{area} was strongly and positively genetically correlated with g_s ($r = 0.850$), suggesting that an increase in photosynthetic rate would also be accompanied by an increase in stomatal conductance, and

A_{area} was negatively correlated with SLA ($r = -0.587$). WUE and g_s had a negative correlation. In *S. salicaria*, carbon assimilation is maintained in such a way that open stomata increase stomatal conductance and CO_2 uptake, but also lead to high transpiration rates and low WUE (Geber & Dawson, 1990). Genetic correlations between ecophysiological traits and those relating to morphology (stem and inflorescence number) were not significant, and may indicate that these traits evolve independently of one another, although indirect associations involving intermediate traits cannot be discounted.

In *S. adamantis*, females exhibited detectable heritability only for g_s , and hermaphrodites had no detectable heritability for any ecophysiological trait. Given these low heritabilities, it would be difficult for ecophysiological traits other than g_s in *S. adamantis* to respond rapidly to direct selection.

The presence of significant narrow-sense heritabilities for stomatal conductance in both species is notable, given that instantaneous measures are extremely plastic, making it difficult to detect genetic effects. Although genotype \times environment interactions might differ between the glasshouse and natural field environments, the presence of heritable traits in this experiment suggests that such traits may also be heritable under field conditions. The narrow-sense heritabilities of g_s in hermaphrodites of *S. salicaria* ($h^2 = 0.38$) and females of *S. adamantis* ($h^2 = 0.39$) were relatively high compared with the broad-sense estimate of g_s in *Cakile edentula* ($H^2 = 0.05$, Dudley, 1996) but lower than the narrow-sense estimate in hermaphrodites of gynodioecious *L. siphilitica* ($h^2 = 0.49$, Caruso *et al.*, 2005) as well as the broad-sense estimate in *Polygonum arenastrum* ($H^2 = 0.71$, Geber & Dawson, 1997). Our value of narrow-sense heritability of the photosynthetic rate (A_{area}) in *S. salicaria* ($h^2 = 0.25$) was higher than the narrow-sense estimate of the same trait in *P. lanceolata* ($h^2 = 0.05$, Tonsor & Goodnight, 1997) and the broad-sense estimate in *Cakile edentula* ($H^2 = 0.097$, Dudley, 1996), but was lower than the narrow-sense estimate in *L. siphilitica* ($h^2 = 0.43$, Caruso *et al.*, 2005) as well as the broad-sense estimate in *Polygonum arenastrum* ($H^2 = 0.87$, Geber & Dawson, 1997). Instantaneous estimates of WUE in our study and most others generally exhibited lower levels of heritable variation, ranging from 0 to 0.13, regardless of whether measured as A/g_s (H^2 ; Dudley, 1996) or A/E (h^2 ; Tonsor & Goodnight, 1997). The exception was *L. siphilitica*, in which narrow-sense heritable variation in WUE was 0.45 as measured by A/g_s (Caruso *et al.*, 2005). Measures of traits responding over a longer time span, such as carbon-isotope discrimination (Δ), an integrated measure of WUE, have typically detected moderate-to-high estimates of broad-sense (0.20–0.81: Schuster *et al.*, 1992; Donovan & Ehleringer, 1994) or narrow-sense heritabilities (0.54: Johnsen *et al.*, 1999). Instantaneous measures may be so plastic that environmental differences, even in controlled glasshouse conditions, may swamp more subtle genetic effects. Despite these possibilities, environmental conditions and ecophysiological measurements in the current study were consistent enough for

significant heritabilities to be detected in several traits. Power of the REML models was sufficiently high in our experiment that all cases of heritability estimates > 0.28 were significantly different from zero.

Several estimates of heritable variation in both *Schiedea* species were very low because of the lack of additive genetic variation (V_A) for those traits, as indicated by the low coefficients of variation. In these cases, strong prior selection or genetic drift may have eliminated additive genetic variation, suggesting that these species may not evolve greater sexual dimorphism. The historically small population size for *S. adamantis* also may have reduced quantitative genetic variation. *Schiedea adamantis* had a lower number of alleles per locus (1.56), percentage of polymorphic loci (22.2%), and expected proportion of heterozygous loci per individual (0.077) than *S. salicaria* (2.22, 66.7%, 0.303, respectively; Weller *et al.*, 1996). Loss of genetic variation following population bottlenecks is well known, although the effects of bottlenecks on quantitative genetic variation in plant populations are less well understood (Reed & Frankham, 2001).

Genetic correlations between sexes Genetic correlations between physiological traits expressed in different sexes may be particularly important in the early stages of the evolution of gynodioecy. Eckhart (1999) suggested that when females are rare in populations, as in *S. salicaria*, their genes are rarely exposed to selection, so that evolution of traits in females is dominated by selection on those genes in hermaphrodites via correlated traits. Sex differences in a given trait may reflect pleiotropic effects involving the male-sterility gene as well as selection on hermaphrodites, rather than the independent evolution of traits in females and hermaphrodites (Eckhart, 1999). In *S. salicaria*, ecophysiological traits in hermaphrodites with significant or marginally significant heritable variation (A_{area} , g_s and SLA) were correlated with several traits in females. SLA in females was positively correlated with SLA in hermaphrodites (Table 4). A_{area} in hermaphrodites was negatively correlated with SLA in females ($r = -0.48$, $P = 0.003$), suggesting that selection for higher A_{area} in hermaphrodites could result in the lower SLA in females. Thus in the early stages of gynodioecy, selection on females via correlated selection on hermaphrodites is plausible in *S. salicaria*, but probably involves a complex matrix of correlated traits. In *S. adamantis*, with a higher frequency of females, traits in females are more likely to evolve independently of selection on hermaphrodites because more genes are exposed to direct selection (Eckhart, 1999). In females of *S. adamantis*, only g_s was heritable and, not surprisingly, there were few significant correlations between ecophysiological traits in females and hermaphrodites.

Implications for studies of sexual dimorphism in plants The evolution of dimorphic breeding systems often involves changes in floral morphology, but changes in ecophysiological traits

may also occur, particularly when habitat shifts accompany the evolution of separate sexes. Although narrow-sense heritabilities may be difficult to detect in ecophysiological traits because of their great plasticity, these ecophysiological traits must have responded to selection in the past to account for present differences in habitat and physiology within *Schiedea* (T.E. Dawson and co-workers, unpublished data). Furthermore, lack of heritable variation in some traits such as WUE in hermaphrodites of *S. adamantis* may reflect past strong selection for these traits during adaptation to dry habitats. The extent of differentiation of separate sexes is important because heritable variation may be found only in the more common sex during early evolutionary stages, while independent selection on ecophysiological traits in both sexes may only occur once females have increased in frequency. This may explain why significant sex differences in ecophysiological traits are often detected in fully dioecious species (Dawson & Ehleringer, 1993; Marshall *et al.*, 1993; Gehring & Monson, 1994; Laporte & Delph, 1996; Hogan *et al.*, 1998; Obeso *et al.*, 1998), but not as frequently in gynodioecious *S. salicaria* and *S. adamantis*. Further investigation is needed in other gynodioecious species with nuclear inheritance of male sterility, as well as in gynodioecious species with nuclear-cytoplasmic inheritance where gynodioecy may be evolutionarily stable (Webb, 1999).

Ecophysiological traits, especially carbon assimilation, are important components of resource acquisition, which is often assumed to be equivalent in the sexes during the evolution of dimorphism (Charlesworth & Charlesworth, 1978; Charnov, 1979, 1982; Sato, 2002; but see Seger & Eckhart, 1996 and references therein). This assumption appears to be supported in *S. adamantis*, where there are few differences in instantaneous measures of resource acquisition between the sexes. In *S. salicaria*, however, the sexes differed in A_{mass} and SLA. In most models for the evolution of sexual dimorphism, females and hermaphrodites (and later, males) are thought to be similar in their ability to obtain resources, but vary in their allocation of resources to male and female function. These models assume a static resource pool through time and space, but in natural environments microsite differences in light and moisture levels may be common. Temporal fluctuations in the resource pool are also likely if females periodically invest more in reproduction and increase the amount or capacity of carbon-importing tissue, resulting in a larger resource pool over time (Delph & Meagher, 1995; Laporte & Delph, 1996). Although significant sex differences in most ecophysiological traits were not detected in *Schiedea* under well watered glass-house conditions, differences may become more apparent in different environments where water is frequently a limiting factor, or during later life stages in this perennial species. Further studies combining knowledge of the resource pool, short and long-term measures of acquisition, biomass, and fitness for each sex may result in better understanding of the evolution of dimorphic breeding systems such as gynodioecy.

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