American Journal of Botany 91(12): 2030–2040. 2004.

ARCHITECTURAL EFFECTS MIMIC FLORAL SEXUAL DIMORPHISM IN *SOLANUM* (SOLANACEAE)[1]

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Factors underlying apparent floral sexual dimorphism were examined in six species of andromonoecious *Solanum* section *Lasiocarpa* (Solanaceae). Both multivariate and univariate analyses show that hermaphroditic flowers are significantly larger than staminate flowers for all features measured. Thus, flowers could be characterized as sexually size dimorphic. However, when size variation due to flower position (architecture) is controlled experimentally, differences between the floral genders for the nongynoecial characters disappear; there is no difference in corolla or androecium size. Staminate flowers appear to be generally smaller than hermaphroditic flowers, not because of any difference related to primary sexual function, but because they tend to occur in the distal regions of each inflorescence. In contrast, significant differences between hermaphroditic and staminate flowers for primary female traits (ovary, style, and stigma) remain after controlling for position: the two floral types are truly dimorphic for these characters. We show that consideration of architectural effects can direct and refine hypotheses concerning the evolution of andromonoecy. More generally, if architectural effects on flower size are common among taxa with unisexual flowers, then these effects may contribute to the common perception of size dimorphism in taxa with unisexual flowers.

Key words: andromonoecy; architecture; flower morphology; positional effects; sexual dimorphism; unisexual flowers; *Solanum*.

Among taxa with unisexual flowers, sexual dimorphism of flowers is common (Darwin, 1877; Lloyd and Webb, 1977; Delph, 1996; Delph et al., 1996; Eckhart, 1999). In particular, sexual dimorphism of corolla size is well documented and has played an important role both in the development of theory underlying sex allocation models and in stimulating empirical research in plant evolutionary ecology. The widespread distribution of floral size dimorphism (occurring in 85% of species with unisexual flowers; Delph et al., 1996) may suggest common underlying explanations for the evolution of sexual size dimorphism, and indeed, a variety of hypotheses have been proposed (summarized in Delph et al., 1996). These range from ''nonfunctional'' hypotheses that postulate developmental correlations between stamens and corolla (Darwin, 1877; Plack, 1957, 1958) to ''functional'' hypotheses that emphasize presumptive biological roles for the perianth in protection (Bawa and Opler, 1975) and pollinator attraction (Bell, 1985) or deal with optimizing resource allocation for male or female function (Eckhart, 1992; Ashman, 1994; Costich and Meagher, 2001; Miller and Venable, 2003).

In a broad survey of monoecious and dioecious species, Delph (1996) and Delph et al. (1996) considered several explanations for the evolution of perianth size dimorphism. Although they found little support for the broad applicability of the developmental correlations hypothesis, the pattern of floral size dimorphism was generally consistent with the hypotheses that selection for male function or for protection of developing reproductive organs drives the evolution of floral sexual dimorphism. However, many of the basic assumptions underlying these hypotheses remain only partially supported or unexplored (Wilson et al., 1994; Conner et al., 1996a, b; Campbell, 2000; Elle and Meagher, 2000), and there are sufficient deviations from predictions to suggest that other factors also operate on the expression of sexual size dimorphism (summarized in Eckhart, 1999). Therefore, we believe that additional explanations of floral size dimorphism should be considered. Here, we explore the possibility that two additional and previously overlooked developmental features, architectural effects and developmental plasticity, may contribute to perianth size dimorphism. Because these features can mimic true sexual dimorphism, they can erroneously provide support for functional hypotheses where no causal relationships exist.

An important component of flower size variation is floral position within inflorescences and inflorescence position within the overall architecture of the plant (Diggle, 1995). Analyses of 65 species in 27 families show significant intra-individual variation in flower size due solely to differences in flower position within inflorescences (Diggle, 2003). Most of these examples involve taxa that produce only hermaphroditic flowers, however in taxa that bear unisexual flowers, the different flower types are often located in distinct positions within inflorescences or within the overall architecture of individuals (Cox, 1988; Waller, 1988). For example, in many monoecious and andromonoecious species, staminate flowers are produced distally whereas female or hermaphroditic flowers are basal within the same inflorescence (Matkze, 1938; Bell, 1971; Hopkins, 1984; Willson and Ruppel, 1984; Solomon, 1985; Cox, 1988; Diggle, 1993; Hoc et al., 1994; Ladd, 1994; Emms et al., 1997; Elle, 1998; Krupnick and Weiss, 1998; Manicacci and Despres, 2001; Miller and Diggle, 2003). In other taxa, the flower types may be segregated among different inflorescences (Jones, 1936; Bell, 1971; Abul-Fatih and Bazzaz, 1979; Lovett Doust, 1980; Pellmyr, 1986; Spalik and Woodell, 1994). Another pattern, common among monoecious and di-

[1] Manuscript received 28 January 2004; revision accepted 26 August 2004.

The authors thank C. Heiser, L. Bohs, and the Botanical Garden of Nijmegen for seed accessions; T. Lemieux for providing valuable advice and support regarding greenhouse space; H. Bechtold and K. Ryerson for assisting with data collection; R. Khorsand, T. Forbis, C. McGraw, and M. Allsop for assistance in the greenhouse; the Department of E. E. Biology at the University of Colorado for greenhouse space; and W. Friedman for comments on earlier drafts of the manuscript. This work was supported by grants from the University of Colorado and the National Science Foundation DEB 9982489 to P.K.D.

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TABLE 1. The six taxa in *Solanum* section *Lasiocarpa* investigated in this study including voucher information. For three of the species, staminate flower production was phenotypically plastic with regard to fruit set and genotypes in the plus-fruit treatment produced a significantly greater proportion of staminate flowers than identical genotypes lacking fruit in the no-fruit treatment. Production of staminate flowers by the remaining three species was invariant with respect to fruit set (data analysis in Miller and Diggle, 2003).

Species	Voucher	No-fruit[a]	Plus-fruit[b]	Plasticity[c]
S. candidum	*J. S. Miller & P. K. Diggle 01* COLO	0.03	0.15	1.31 (*)
S. ferox var. *lasiocarpum*	*J. S. Miller & P. K. Diggle 02* COLO	0.06	0.20	1.03 (*)
S. stramonifolium var. *inerme*	*J. S. Miller & P. K. Diggle 03* COLO	0.01	0.10	1.61 (*)
S. pectinatum	*J. S. Miller & P. K. Diggle 04* COLO	0.66	0.79	0.17 (ns)
S. pseudolulo	*J. S. Miller & P. K. Diggle 05* COLO	0.39	0.40	0.02 (ns)
S. quitoense	*J. S. Miller & P. K. Diggle 06* COLO	0.59	0.66	0.11 (ns)

[a] Mean proportion of staminate flowers per inflorescence for plants of the no-fruit treatment.
[b] Mean proportion of staminate flowers per inflorescence for plants of the plus-fruit treatment.
[c] Plasticity of sexual expression was quantified as the difference between the proportion of staminate flowers produced within inflorescences on plants with fruit and those without fruit, divided by the average across both treatments. The values range from 0 (treatment means equal; no plasticity) to 2 (maximum difference between the means; maximum plasticity). The symbol in parentheses indicates the significance level of an analysis of variance for the effect of fruit set on staminate flower production (*) = $P < 0.05$, (ns) = not significant.

oecious taxa, is the production of solitary female flowers and complex multiflowered staminate inflorescences (Whitaker and Davis, 1962; Bawa, 1980; Delasalle, 1992; Cronquist, 1993; Costich, 1995). These examples demonstrate that architectural effects are as likely to occur among species producing unisexual flowers as in taxa with only hermaphroditic flowers. Further, it is conceivable that size differences between the sexual phenotypes (e.g., male and female flowers in monoecious species, or male and hermaphroditic flowers in andromonoecious species) in these species could be a consequence of flower position rather than a direct effect of floral gender.

Plastic responses to variation in resource availability may also explain size differences between sexually dimorphic flowers. Fruit set by early flowers is known to result in the reallocation of resources away from the growth of later initiated flowers (Lloyd, 1980; Stephenson, 1981). Often, the result of such resource preemption is decreased size of flowers that are initiated later in development (reviewed in Diggle, 1995). Obviously, in an analysis of dioecious species, only females will be subject to this plastic response. Consequently, if sampling of female flowers follows fruit initiation, then differences in flower size between females and non-fruit bearing males may be due to plasticity of flower size in females rather than to inherent gender-based differences. Likewise, in monoecious or andromonoecious species, if the sexual phenotypes are produced at different times or at different distances from the resource supply, then one flower type or the other will be more subject to plastic variation due to resource preemption.

In this paper, we address the effects of architecture and plastic responses to resource preemption on the expression of floral sexual dimorphism in andromonoecious *Solanum* section *Lasiocarpa* (Solanaceae). Previous work on andromonoecious *Solanum* has demonstrated that there is striking dimorphism for flower size. Specifically, staminate flowers are smaller than hermaphroditic flowers in a number of species (Smith, 1931; Martin, 1972; Reddy and Bahadur, 1977; Baksh et al., 1979; Dulberger et al., 1981; Solomon, 1986; Whalen and Costich, 1986; Anderson and Symon, 1989; Diggle, 1991). Species of *Solanum* section *Lasiocarpa* are especially suited to analyses of the effects of architectural variation and plasticity on flower size dimorphism. Flowers are produced in elongate inflorescences, and staminate flowers, when produced, are initiated distally within each inflorescence, such that floral position has the potential to influence the morphology of those flowers. In addition, the production of staminate flowers in some species is a phenotypically plastic response to the presence of developing fruit (Diggle, 1993; Miller and Diggle, 2003; J. S. Miller and P. K. Diggle, unpublished data). Thus, the smaller size of staminate flowers may also be the result of resource preemption rather than an expression of sexual dimorphism.

Differences in morphology between hermaphroditic and staminate flowers for both primary (androecium and gynoecium) and secondary (corolla) sexual traits for six species in *Solanum* section *Lasiocarpa* are quantified to address the following questions. Are hermaphroditic flowers larger than staminate flowers, and if so, for which floral traits? To what degree are size differences in floral structures explained by architectural effects (flower position), and does the floral sexual size dimorphism remain after correcting for architectural variation? Does resource preemption by developing fruit (i.e., plasticity) contribute to size variation in floral structures, and do these effects differ between species with fixed vs. phenotypically plastic production of staminate flowers?

MATERIALS AND METHODS

Study species—The 12 species of *Solanum* section *Lasiocarpa* clearly form a monophyletic group (Heiser, 1972, 1987; Whalen and Caruso, 1983; Bernardello et al., 1994; Bruneau et al., 1995; Bohs, 2004). They are sexually reproducing, self-compatible, and andromonoecious. Sexual expression (the proportion of flowers that are staminate) varies considerably among species ranging from near zero (<1%) to over 60% staminate flowers per inflorescence among the seven species studied to date (Diggle, 1993; Miller and Diggle, 2003; J. S. Miller and P. K. Diggle, unpublished data). Flowers of *Solanum* section *Lasiocarpa* are slightly zygomorphic and five-merous, except for the gynoecium, which is bicarpellate, and are borne in monochasial cymes that resemble racemes at maturity. Within inflorescences, flowers mature acropetally and each inflorescence generally has more than one open flower at any given time. Inflorescences are produced sequentially along branches and multiple inflorescences per branch may bear open flowers simultaneously.

Six species of *Solanum* section *Lasiocarpa* are included in the current study: *S. candidum*, *S. ferox* var. *lasiocarpum*, *S. stramonifolium* var. *inerme*, *S. pectinatum*, *S. pseudolulo*, and *S. quitoense*. Voucher specimens are housed at the University of Colorado herbarium (COLO; Table 1). There is considerable variation among species in both flower size and the number of flowers per inflorescence. In addition, manipulation of fruit set on clonal replicates of multiple genotypes for each of these species demonstrated interspecific variation for phenotypic plasticity. The strongly andromonoecious species, *S. pseudolulo*, *S. pectinatum*, and *S. quitoense*, were not plastic and produced a large proportion of staminate flowers regardless of fruiting treatment, whereas *S. candidum*, *S. ferox*, and *S. stramonifolium* were phenotypically plastic and

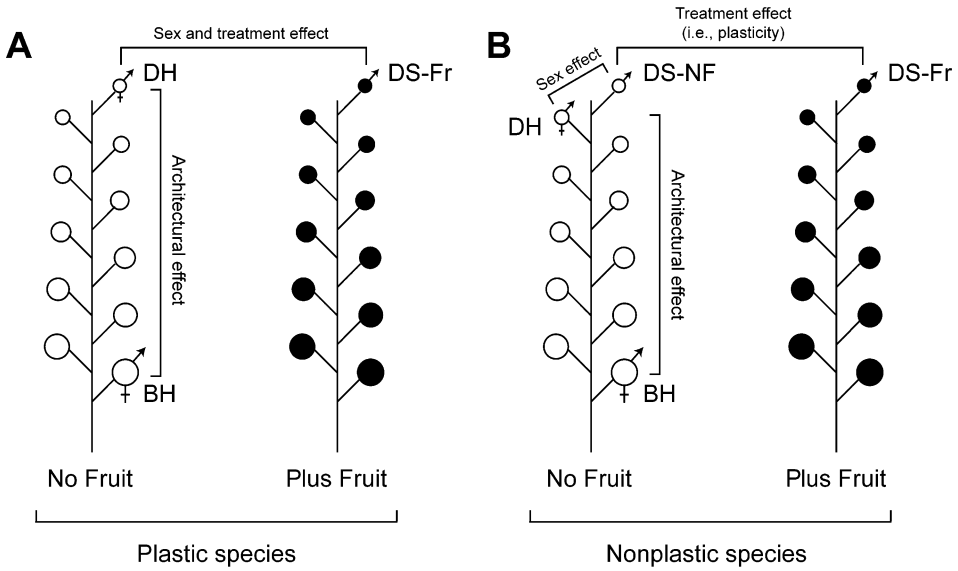

Fig. 1. Experimental design used to differentiate architectural variation, plastic effects, and sexual dimorphism in (A) plastic and (B) nonplastic species of *Solanum*. Plants are assigned to one of two treatments; either a treatment in which no flowers are pollinated and fruit are not allowed to mature (no-fruit), or a treatment in which all flowers within inflorescences are pollinated and allowed to mature fruit (plus-fruit). Comparison of flowers from different positions within inflorescences in the no-fruit treatment measures variation due to architectural effects. Comparison of flowers in equivalent positions between the two treatments measures the effect of fruiting treatment or plasticity. Additionally, for the nonplastic species, comparisons of distal hermaphroditic and staminate flowers in the no-fruit treatment controls for both position and treatment and measures differences in morphology due solely to sexual phenotype. BH = basal hermaphroditic flower of the no-fruit treatment; DH = distal hermaphroditic flower of the no-fruit treatment; DS-Fr = distal staminate flower of the plus-fruit treatment; DS-NF = distal staminate flower of the no-fruit treatment.

produced significantly more staminate flowers in the presence of developing fruit (Table 1; Miller and Diggle, 2003; J. S. Miller and P. K. Diggle, unpublished data).

Although plasticity of the six species has been characterized only with respect to the effect of fruit set on staminate flower production, for convenience we will refer to the species as either plastic or fixed (i.e., nonplastic) without continued reference to the basis for plasticity of sexual expression. Similarly, although there is variation among the plastic species in the magnitude of response to fruit set, we will not refer to the degree of plasticity here.

Experimental design—Plants were grown from seed and replicated by vegetative cuttings to produce genetically identical plants. The number of clonally replicated genotypes used for each species ranged from six (*S. ferox* var. *lasiocarpum*) to 10 (*S. stramonifolium* var. *inerme*), and the number of clonal replicates per genotype ranged from four to eight. Plants were maintained in 3-gallon pots containing a 2 : 1 mix of Fafard Growing Mix #2 (Conrad Fafard, Inc., Agawam, Massachusetts, USA) to Persolite (Persolite Products, Inc., Florence, Colorado, USA) plus Osmocote 13–13–13 slow-release fertilizer (Scotts Company, Marysville, Ohio, USA), and were watered daily with 150–200 ppm of Excel Magnitrate fertilizer (Scotts Company, Marysville, Ohio, USA). Plants were grown in neighboring greenhouse rooms, which were maintained at 21°C. For each species, the experiment (described below) was entirely replicated in each greenhouse room.

Replicate plants for each genotype were assigned one of two treatments: plus-fruit or no-fruit (Fig. 1). All flowers on plants in the plus-fruit treatment were pollinated every other day with a mixture of pollen from ≥3 conspecific donors. Hermaphroditic flowers remained open for 2–4 d, such that all hermaphroditic flowers were pollinated at least once. In contrast, plants in the no-fruit treatment were not pollinated, and any autogamously produced fruit were removed shortly after their initiation. Total plant resource status is associated with fruit production, and plants with developing fruit have fewer resources available for growth and continued reproduction than plants with no developing fruit (Lloyd, 1980; Stephenson, 1981). Thus, experimental manipulation of plant fruiting status is an effective, biologically relevant way to manipulate total plant resource status. Experimental manipulation of plant resource status was necessary to promote staminate flower production in the plastic species and to test for plastic changes in floral phenotypes due to resource effects of developing fruit. Because inflorescences are produced continuously, floral buds, flowers, and developing fruit occur simultaneously on each of multiple branches per plant and resource preemption by early fruit can potentially affect the development of later initiated flowers and fruits.

Variation in floral form—Recently opened flowers (≤48 h old) were collected and fixed in FAA (Berlyn and Miksche, 1976) before being transferred to 70% EtOH for storage. Flower collections differed for the plastic and nonplastic species. For the plastic species (*S. candidum*, *S. ferox*, and *S. stramonifolium*), the distribution of flower types differs significantly between plants of the no-fruit and plus-fruit treatments. Plants of the no-fruit treatment bear predominantly hermaphroditic flowers at all positions, whereas plus-fruit plants bear hermaphroditic flowers in basal positions and staminate flowers in distal positions within each inflorescence. For these species, hermaphroditic flowers were collected from basal (BH) and distal (DH) positions within inflorescences from plants in the no-fruit treatment and staminate flowers were collected from distal positions of plus-fruit plants (DS; Fig. 1A). For the nonplastic species (*S. pectinatum*, *S. pseudolulo*, and *S. quitoense*), the distribution of flower types is statistically indistinguishable for the two treatments and qualitatively resembles that of the plus-fruit plants of the plastic species (Miller and Diggle, 2003). Although staminate flowers predominated in distal positions, sufficient numbers of hermaphroditic flowers were produced in distal positions such that we could include them in the sample. Hermaphroditic flowers were collected from basal (BH) and distal (DH) positions in the no-fruit treatment, and staminate flowers from distal positions on both no-fruit (DS-NF) and plus-fruit (DS-Fr) plants (Fig. 1B). Flowers were sampled from all genotypes for each of the species. Flowers were collected from September 2000 to May 2001 for *S. candidum*, *S. pseudolulo*, and *S. quitoense*, from December 2001 to March 2002 for *S. ferox*, and from July 2002 to September 2002 for *S. stramonifolium* and *S. pectinatum*. Flowers were dissected and measured either with digital calipers or under a Zeiss Stemi SV-11 dissecting microscope equipped with an ocular micrometer. For each flower, eight mea-

TABLE 2. Eigenvalues, the proportion of variance explained, and eigenvectors for the first two principal components of the analysis of eight floral characters for six *Solanum* species.

	PC1	PC2
Eigenvalue	5.66	1.17
Proportion of variance explained	0.71	0.15
Eigenvectors:		
Dorsal petal length	0.388	−0.286
Doral petal width	0.386	−0.206
Anther length	0.350	−0.345
Anther width	0.371	−0.320
Style length	0.233	0.680
Stigma width	0.370	0.276
Ovary length	0.377	0.260
Ovary width	0.327	0.219

surements were made: length and width of the dorsal petal, anther length and width (filaments in these species are minute and do not contribute to stamen length), style length, stigma width, and ovary length and width. Although staminate flowers do not produce fruit, they do possess rudimentary gynoecia, which were measured as in hermaphroditic flowers.

Statistical analyses—A principal components analysis was used to summarize variation in the floral characters (JMP 5.0.1a, SAS Institute, 1989–2002). Measurements of replicate flowers of the same flower identity (a variate that indicates both the position and sex of each flower: BH, DH, or DS for the plastic species; BH, DH, DS-NF, or DS-Fr for the fixed species; see Fig. 1) were averaged for each genotype within species and these means were natural log transformed prior to the principal components analysis. We used a general linear model with species, sex, and their interaction as effects to assess variation in size and shape as defined by the first two principal components. Tukey's honestly significant different (HSD) multiple-comparison procedure was used to compare all species pairwise combinations (JMP 5.0.1a, SAS Institute, 1989–2002).

For each species, univariate analyses were also carried out for each floral character to assess the contributions of architecture, plasticity, and flower sex to size variation. Specifically, data for each floral character were analyzed using separate general linear models that included the fixed effect of flower identity (as defined above; JMP 5.0.1a, SAS Institute, 1989–2002). For each trait, we used a linear contrast to test whether hermaphroditic flowers (pooled over all flower positions) were larger than staminate flowers (pooled over all treatments). Tukey's HSD multiple-comparison procedure was used in separate analyses to compare all flower identity categories (JMP 5.0.1a, SAS Institute, 1989–2002).

Subsequent data analyses and interpretation differed slightly for the plastic and nonplastic species. For all species, significant differences between BH and DH flowers of nonfruiting plants is a measure of architectural variation (Fig. 1). In the plastic species, comparison of DH of nonfruiting and DS of fruiting plants controls for position and measures both plastic responses to the fruiting treatment (i.e., resource preemption) and floral sexual dimorphism (Fig. 1A). In the nonplastic species, because both hermaphroditic and staminate flowers occurred in distal positions of the nonfruiting treatment, plasticity can be separated from sexual dimorphism. Comparison of DS flowers from the two treatments holds position and gender constant and is a measure of plasticity, whereas comparison of DS and DH flowers from nonfruiting plants holds position and treatment constant and is a measure of floral sexual dimorphism (Fig. 1B).

RESULTS

Morphology of hermaphroditic and staminate flowers—*Principal components analysis*—The first principal component (PC1) accounted for 71% of the total variation in the data and was an indicator of overall flower size (Table 2). There was significant variation among species for PC1 ($F_{5,\ 147} = 284.0$, $P < 0.0001$). Flowers from *S. pectinatum* and *S. quitoense* were significantly larger than flowers from all other species, and the species with the smallest flowers was *S. stramonifolium* (Fig. 2). Hermaphroditic flowers were larger than staminate flowers both overall ($F_{1,\ 147} = 386.15$, $P < 0.0001$) and within each species (Fig. 2B, upper panel). The interaction between species and sex was not significant ($F_{5,\ 147} = 1.8$, $P = 0.1164$), indicating that the magnitude of size dimorphism was similar among the species.

Principal component 2 (PC2) explained 15% of the total variation and the two floral sexual phenotypes segregated along this axis (Fig. 2A). PC2 was strongly positively associated with style length and to a lesser degree stigma width, ovary length, and ovary width, whereas it was weakly negatively associated with petal and anther lengths and widths (Table 2). Species ($F_{5,\ 147} = 42.63$, $P < 0.0001$), sex ($F_{1,\ 147} = 774.02$, $P < 0.0001$), and their interaction ($F_{5,\ 147} = 6.81$, $P < 0.0001$) were all highly significant for PC2. Hermaphroditic and staminate flowers in *S. pectinatum* and *S. quitoense* showed greater dimorphism for PC2 compared to all other species (Tukey's HSD test; Fig. 2B, lower panel).

Univariate analyses—Analyses of individual traits revealed a pattern similar to the principal components analysis. Hermaphroditic flowers were significantly larger than staminate flowers for all floral traits measured, with the single exception of anther width in *S. stramonifolium* (Table 3). However, there were differences in the magnitude of sexual dimorphism for specific floral structures. Style length ranged from 2.8 times larger in hermaphroditic compared to staminate flowers of *S. stramonifolium* to 5.9 times larger in *S. quitoense* (Table 3). Similarly, on average for all species, ovaries were 1.6 times longer and 1.4 times wider, and stigmas were 1.7 times wider in hermaphroditic than staminate flowers. In contrast, anther size, although statistically different between hermaphroditic and staminate flowers, showed considerably less dimorphism. Anthers in hermaphroditic flowers were on average only 1.07 times longer and wider than those in staminate flowers. Petal size was 1.1 times longer and 1.2 times wider in hermaphroditic flowers averaged across the six species.

Architectural effects on floral morphology—Architectural effects were common among the *Solanum* species studied. Within inflorescences of unpollinated plants, distal hermaphroditic flowers were significantly smaller than basal hermaphroditic flowers for 73% of the floral characters measured (Table 4), however, these effects varied across species. For example, in three species (*S. candidum*, *S. stramonifolium*, and *S. pseudolulo*), distal flowers were smaller than basal flowers for seven of the eight floral characters. In contrast, *S. pectinatum* and *S. quitoense* showed architectural variation for only half of the floral characters (Table 4). Ovary length and width showed strong architectural variation; distal hermaphroditic flowers had significantly smaller ovaries than did basal hermaphroditic flowers for all species (Table 4). For two of the three plastic species, styles in basal hermaphroditic flowers were longer than those in distal hermaphroditic flowers. In contrast, none of the nonplastic species had significant architectural variation for style length (Table 4).

When architectural variation is controlled by comparison of DH and DS in the plastic species, several differences between the floral sexual phenotypes disappear. For example, there are

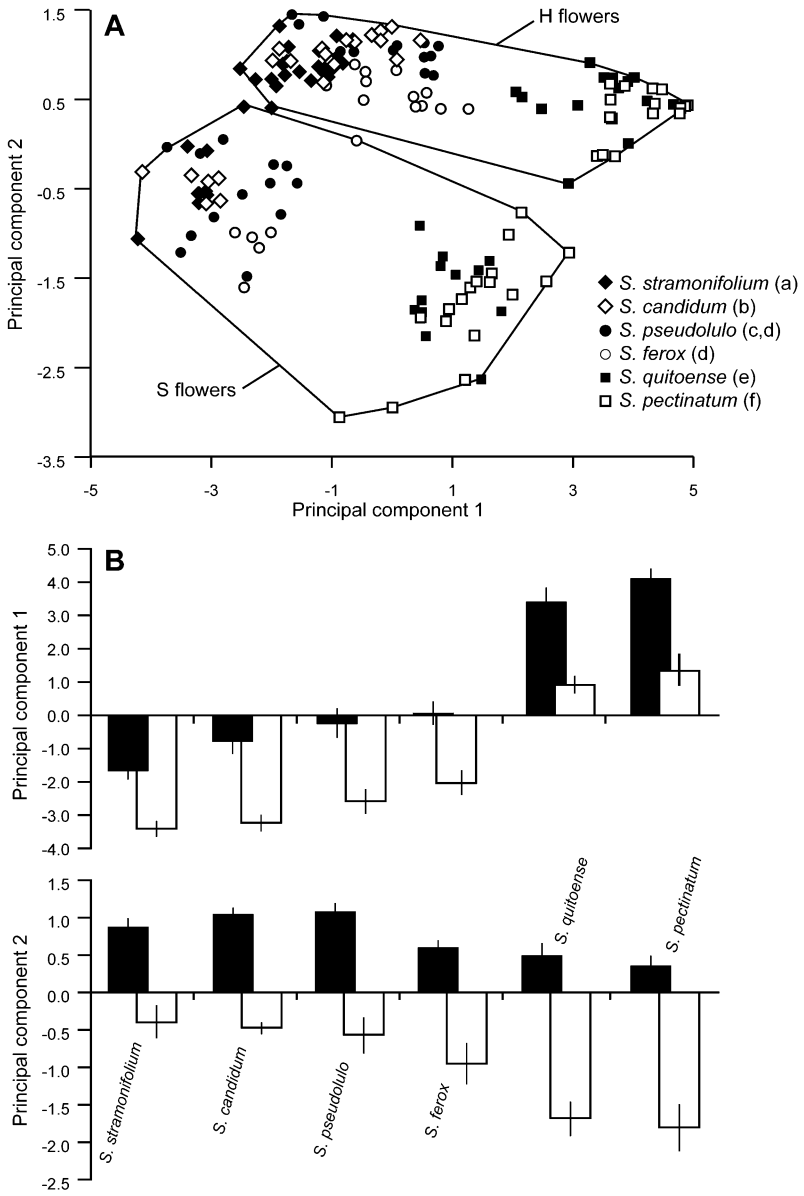

Fig. 2. (A) Scatterplot of the first two principal components of the analysis of eight floral characters of six *Solanum* species. Species are identified by symbols and are arranged from smallest (*S. stramonifolium*) to largest (*S. pectinatum*). Letters in parentheses following the species names indicate significance; species sharing the same letter are not statistically significantly different from one another for principal component 1 using Tukey's HSD multiple-comparison test (see Materials and Methods). (B) Values of PC1 and PC2 for hermaphroditic (shaded bars) and staminate (open bars) flowers for each species. Error bars are 1 SD.

few significant differences that remain for petal or anther characters for these species (compare Tables 3 and 4). After correcting for architectural variation, only petal width and anther length in *S. candidum* and anther length in *S. stramonifolium* showed significant differences between hermaphroditic and staminate flowers (Table 4). It is important to recognize that these differences could be due to plastic responses to the differing resource status of the plants, sexual dimorphism, or both. As expected, differences in the four gynoecium characters remained; they were significantly reduced in staminate flowers for all species examined, likely reflecting the functional differences between the two floral phenotypes.

In the nonplastic species, it was possible to control for both architectural variation and fruiting treatment. Comparison of distal hermaphroditic and staminate flowers in the no-fruit treatment (DH vs. DS-NF, Table 4) identifies those character differences associated with either primary sexual function or sexual dimorphism. For all three of the fixed species, the four gynoecial characters were significantly smaller in staminate compared to hermaphroditic flowers (Table 4). In addition to the gynoecium, anthers of staminate flowers were smaller than those of hermaphroditic flowers for *S. pectinatum*, but not for *S. pseudolulo* or *S. quitoense*. In contrast to the primary sexual organs, there were no significant differences between distal hermaphroditic flowers and distal staminate flowers for either petal length or width for any of the nonplastic species (Table 4).

TABLE 3. Means (±1 SD) of eight floral characters for hermaphroditic (H) and staminate (S) flowers from six *Solanum* species. Results of linear contrasts indicate that hermaphroditic flowers are larger than staminate flowers for all traits with one exception (anther width in *S. stramonifolium*). For each trait, the ratio of hermaphroditic to staminate structure size is presented. Units are in millimeters.

Floral character	Species	Contrast	Pooled H	Pooled S	H:S
Petal length	*S. candidum*	$F_{1,72} = 8.91$*	14.44 ± 1.81	12.70 ± 2.73	1.14
	S. ferox	$F_{1,81} = 6.64$*	16.64 ± 2.92	15.20 ± 2.21	1.09
	S. stramonifolium	$F_{1,99} = 36.74$***	12.13 ± 1.22	10.86 ± 0.92	1.12
	S. pectinatum	$F_{1,117} = 29.41$***	28.11 ± 4.10	24.55 ± 3.42	1.15
	S. pseudolulo	$F_{1,102} = 13.28$**	15.28 ± 2.93	13.53 ± 2.32	1.13
	S. quitoense	$F_{1,99} = 9.34$*	22.62 ± 4.45	20.06 ± 3.12	1.13
Petal width	*S. candidum*	$F_{1,72} = 20.32$***	6.81 ± 1.02	5.45 ± 1.23	1.25
	S. ferox	$F_{1,81} = 12.97$**	7.42 ± 1.23	6.63 ± 0.88	1.12
	S. stramonifolium	$F_{1,99} = 35.97$***	6.55 ± 0.77	5.71 ± 0.69	1.15
	S. pectinatum	$F_{1,117} = 15.78$***	10.46 ± 1.77	9.33 ± 1.56	1.12
	S. pseudolulo	$F_{1,102} = 18.98$***	6.52 ± 1.35	5.58 ± 1.15	1.17
	S. quitoense	$F_{1,99} = 12.12$**	10.52 ± 2.04	9.28 ± 1.49	1.13
Anther length	*S. candidum*	$F_{1,72} = 59.93$***	7.52 ± 0.37	6.67 ± 0.43	1.13
	S. ferox	$F_{1,81} = 14.63$**	7.63 ± 0.66	7.12 ± 0.39	1.07
	S. stramonifolium	$F_{1,99} = 19.83$***	7.36 ± 0.27	7.05 ± 0.40	1.04
	S. pectinatum	$F_{1,117} = 39.09$***	14.95 ± 0.84	14.03 ± 0.79	1.07
	S. pseudolulo	$F_{1,102} = 13.74$**	6.68 ± 0.57	6.36 ± 0.31	1.05
	S. quitoense	$F_{1,99} = 35.09$***	10.53 ± 0.73	9.73 ± 0.63	1.08
Anther width	*S. candidum*	$F_{1,72} = 14.47$**	2.39 ± 0.17	2.21 ± 0.19	1.08
	S. ferox	$F_{1,81} = 11.85$**	2.97 ± 0.27	2.78 ± 0.19	1.07
	S. stramonifolium	$F_{1,99} = 2.82$, $P < 0.10$	2.37 ± 0.13	2.33 ± 0.09	1.02
	S. pectinatum	$F_{1,117} = 32.55$***	3.69 ± 0.18	3.47 ± 0.25	1.07
	S. pseudolulo	$F_{1,102} = 21.73$***	2.71 ± 0.31	2.49 ± 0.19	1.09
	S. quitoense	$F_{1,99} = 34.96$***	3.96 ± 0.30	3.60 ± 0.30	1.10
Style length	*S. candidum*	$F_{1,72} = 593.89$***	6.65 ± 0.67	1.81 ± 0.80	3.67
	S. ferox	$F_{1,81} = 683.51$***	6.73 ± 0.54	2.17 ± 1.09	3.10
	S. stramonifolium	$F_{1,99} = 722.42$***	7.22 ± 0.74	2.59 ± 1.05	2.79
	S. pectinatum	$F_{1,117} = 1421.92$***	15.12 ± 1.45	2.76 ± 2.07	5.47
	S. pseudolulo	$F_{1,102} = 718.19$***	4.83 ± 0.67	1.35 ± 0.67	3.58
	S. quitoense	$F_{1,99} = 1880.71$***	9.51 ± 1.10	1.60 ± 0.71	5.94
Stigma width	*S. candidum*	$F_{1,72} = 38.16$***	0.62 ± 0.12	0.43 ± 0.11	1.44
	S. ferox	$F_{1,81} = 166.84$***	0.65 ± 0.08	0.38 ± 0.10	1.71
	S. stramonifolium	$F_{1,99} = 115.33$***	0.45 ± 0.07	0.28 ± 0.09	1.61
	S. pectinatum	$F_{1,117} = 198.63$***	0.96 ± 0.12	0.65 ± 0.12	1.47
	S. pseudolulo	$F_{1,102} = 271.15$***	0.62 ± 0.09	0.33 ± 0.10	1.88
	S. quitoense	$F_{1,99} = 338.02$**	0.90 ± 0.15	0.49 ± 0.09	1.84
Ovary length	*S. candidum*	$F_{1,71} = 67.14$***	2.21 ± 0.47	1.27 ± 0.23	1.74
	S. ferox	$F_{1,81} = 88.11$***	2.35 ± 0.40	1.52 ± 0.35	1.55
	S. stramonifolium	$F_{1,99} = 85.52$***	1.95 ± 0.28	1.46 ± 0.22	1.34
	S. pectinatum	$F_{1,117} = 330.76$***	4.17 ± 0.49	2.47 ± 0.58	1.69
	S. pseudolulo	$F_{1,102} = 140.06$***	2.91 ± 0.45	1.94 ± 0.45	1.50
	S. quitoense	$F_{1,99} = 90.14$***	3.55 ± 0.65	2.35 ± 0.60	1.51
Ovary width	*S. candidum*	$F_{1,71} = 79.36$***	2.95 ± 0.38	2.02 ± 0.35	1.46
	S. ferox	$F_{1,81} = 122.12$***	2.74 ± 0.41	1.84 ± 0.33	1.49
	S. stramonifolium	$F_{1,99} = 74.39$***	2.42 ± 0.23	2.04 ± 0.20	1.19
	S. pectinatum	$F_{1,117} = 192.50$***	3.60 ± 0.41	2.56 ± 0.46	1.41
	S. pseudolulo	$F_{1,102} = 103.91$***	3.37 ± 0.40	2.51 ± 0.49	1.34
	S. quitoense	$F_{1,99} = 142.04$***	5.04 ± 0.69	3.66 ± 0.60	1.38

* $P < 0.05$, ** $P < 0.001$, *** $P < 0.0001$.

Plastic effects on floral morphology—In the nonplastic species, comparison of distal staminate flowers between the fruiting and nonfruiting treatments identifies the effects of resource preemption by developing fruit (DS-NF vs. DS-Fr, Table 4). These effects were negligible for most floral characters in the nonplastic species. With the exception of anther length and width in *S. quitoense* and ovary width in *S. pectinatum*, distal staminate flowers in the no-fruit and plus-fruit treatments were indistinguishable (Table 4). Although fruiting treatment did not appear to affect allocation to the sizes of floral structures within flowers, this treatment did have a significant effect on the number of flowers produced per inflorescence or total number of inflorescences for several species (data not shown).

DISCUSSION

Morphological differences between hermaphroditic and staminate flowers—When flowers are grouped according to sexual phenotype and compared, hermaphroditic flowers are significantly larger than staminate flowers for all six species of *Solanum* investigated. Both multivariate (Fig. 2) and univariate analyses (Table 3) show that the sizes of all eight measured floral traits are greater for hermaphroditic compared to staminate flowers (with one exception where there was no difference). The magnitude of the overall size dimorphism was similar among the six species of *Solanum* studied (i.e., the species by sex interaction was not significant for PC1), indi-

TABLE 4. Means (±1 SD) for each floral character of six *Solanum* species. For each floral character within species, means sharing the same superscript do not differ significantly as determined by Tukey's HSD multiple-comparison procedure. Abbreviations indicate position of flowers within inflorescences (B, basal or D, distal), floral sexual phenotype (H, hermaphroditic or S, staminate), and fruiting treatment (NF, no-fruit or Fr, plus-fruit). Units are in millimeters. Comparisons between BH and DH measures variation due to architectural effects. Comparisons of DH-NF and DS-NF measures sexual dimorphism. Comparisons of DS-NF and DS-Fr measures variation due to treatment.

Floral character	Species	BH	DH	DS-NF	DS-Fr
Petal length	*S. candidum*	15.00 ± 1.78 a	13.86 ± 1.68 ab	—	12.70 ± 2.73 b
	S. ferox	18.37 ± 2.41 a	14.90 ± 2.31 b	—	15.20 ± 2.21 b
	S. stramonifolium	12.82 ± 0.80 a	11.40 ± 1.16 b	—	10.86 ± 0.92 b
	S. pectinatum	29.88 ± 3.99 a	26.29 ± 3.40 b	24.65 ± 3.84 b	24.46 ± 3.00 b
	S. pseudolulo	16.54 ± 2.58 a	13.98 ± 2.73 b	13.62 ± 2.52 b	13.40 ± 2.07 b
	S. quitoense	23.50 ± 4.43 a	21.15 ± 4.20 ab	20.53 ± 3.53 b	19.53 ± 2.55 b
Petal width	*S. candidum*	7.18 ± 0.90 a	6.44 ± 1.02 b	—	5.45 ± 1.23 c
	S. ferox	8.24 ± 0.91 a	6.60 ± 0.92 b	—	6.63 ± 0.88 b
	S. stramonifolium	7.00 ± 0.53 a	6.06 ± 0.69 b	—	5.71 ± 0.69 b
	S. pectinatum	11.40 ± 1.59 a	9.48 ± 1.40 b	9.38 ± 1.79 b	9.29 ± 1.31 b
	S. pseudolulo	7.24 ± 1.09 a	5.77 ± 1.19 b	5.72 ± 1.25 b	5.38 ± 0.98 b
	S. quitoense	10.58 ± 2.05 a	10.43 ± 2.08 a	9.57 ± 1.76 ab	8.96 ± 1.05 b
Anther length	*S. candidum*	7.64 ± 0.32 a	7.39 ± 0.39 b	—	6.67 ± 0.43 c
	S. ferox	7.88 ± 0.59 a	7.39 ± 0.64 b	—	7.12 ± 0.39 b
	S. stramonifolium	7.42 ± 0.21 a	7.29 ± 0.31 a	—	7.05 ± 0.40 b
	S. pectinatum	15.14 ± 0.79 a	14.75 ± 0.85 a	13.92 ± 0.76 b	14.14 ± 0.81 b
	S. pseudolulo	6.88 ± 0.34 a	6.47 ± 0.67 b	6.44 ± 0.24 b	6.25 ± 0.38 b
	S. quitoense	10.69 ± 0.84 a	10.25 ± 0.38 ab	9.98 ± 0.58 b	9.45 ± 0.56 c
Anther width	*S. candidum*	2.47 ± 0.16 a	2.31 ± 0.14 b	—	2.21 ± 0.19 b
	S. ferox	3.09 ± 0.25 a	2.85 ± 0.24 b	—	2.78 ± 0.19 b
	S. stramonifolium	2.42 ± 0.09 a	2.32 ± 0.14 b	—	2.33 ± 0.09 b
	S. pectinatum	3.68 ± 0.19 a	3.70 ± 0.17 a	3.45 ± 0.25 b	3.48 ± 0.25 b
	S. pseudolulo	2.87 ± 0.20 a	2.54 ± 0.31 b	2.50 ± 0.22 b	2.49 ± 0.15 b
	S. quitoense	4.08 ± 0.25 a	3.76 ± 0.28 b	3.70 ± 0.20 b	3.48 ± 0.36 c
Style length	*S. candidum*	6.87 ± 0.62 a	6.43 ± 0.66 b	—	1.81 ± 0.80 c
	S. ferox	6.91 ± 0.56 a	6.54 ± 0.45 a	—	2.17 ± 1.09 b
	S. stramonifolium	7.51 ± 0.66 a	6.91 ± 0.69 b	—	2.59 ± 1.05 c
	S. pectinatum	15.44 ± 1.70 a	14.80 ± 1.08 a	2.81 ± 2.58 b	2.72 ± 1.47 b
	S. pseudolulo	4.98 ± 0.54 a	4.67 ± 0.75 a	1.46 ± 0.72 b	1.21 ± 0.60 b
	S. quitoense	9.71 ± 1.19 a	9.18 ± 0.85 a	1.71 ± 0.85 b	1.49 ± 0.50 b
Stigma width	*S. candidum*	0.67 ± 0.12 a	0.56 ± 0.08 b	—	0.43 ± 0.11 c
	S. ferox	0.65 ± 0.08 a	0.66 ± 0.08 a	—	0.38 ± 0.10 b
	S. stramonifolium	0.48 ± 0.07 a	0.42 ± 0.07 b	—	0.28 ± 0.09 c
	S. pectinatum	0.98 ± 0.12 a	0.95 ± 0.13 a	0.64 ± 0.12 b	0.67 ± 0.11 b
	S. pseudolulo	0.67 ± 0.08 a	0.58 ± 0.07 b	0.33 ± 0.12 c	0.33 ± 0.09 c
	S. quitoense	0.98 ± 0.12 a	0.77 ± 0.11 b	0.49 ± 0.10 c	0.48 ± 0.09 c
Ovary length	*S. candidum*	2.45 ± 0.44 a	1.95 ± 0.36 b	—	1.27 ± 0.23 c
	S. ferox	2.49 ± 0.38 a	2.21 ± 0.37 b	—	1.52 ± 0.35 c
	S. stramonifolium	2.07 ± 0.28 a	1.82 ± 0.22 b	—	1.46 ± 0.22 c
	S. pectinatum	4.36 ± 0.51 a	3.98 ± 0.38 b	2.33 ± 0.60 c	2.61 ± 0.53 c
	S. pseudolulo	3.11 ± 0.34 a	2.69 ± 0.46 b	2.06 ± 0.44 c	1.78 ± 0.42 c
	S. quitoense	3.79 ± 0.63 a	3.15 ± 0.44 b	2.43 ± 0.58 c	2.25 ± 0.63 c
Ovary width	*S. candidum*	3.10 ± 0.36 a	2.79 ± 0.33 b	—	2.02 ± 0.35 c
	S. ferox	2.98 ± 0.38 a	2.51 ± 0.30 b	—	1.84 ± 0.33 c
	S. stramonifolium	2.53 ± 0.22 a	2.29 ± 0.17 b	—	2.04 ± 0.20 c
	S. pectinatum	3.75 ± 0.48 a	3.45 ± 0.25 b	2.40 ± 0.49 c	2.72 ± 0.38 d
	S. pseudolulo	3.57 ± 0.28 a	3.15 ± 0.39 b	2.48 ± 0.45 c	2.54 ± 0.56 c
	S. quitoense	5.48 ± 0.40 a	4.31 ± 0.40 b	3.73 ± 0.56 c	3.58 ± 0.65 c

cating that staminate and hermaphroditic flowers within each species were similarly dimorphic (Fig. 2). This was true despite the fact that the included species produced flowers of vastly different sizes. However, there was a significant species by sex interaction for PC2. Hermaphroditic and staminate flowers in the larger flowered species, *S. pectinatum* and *S. quitoense*, showed greater dimorphism for PC2 compared to the other species (Tukey's HSD test; Fig. 2B).

Greater hermaphroditic flower size has been documented for numerous other andromonoecious *Solanum* (e.g., *S. hirtum*, Diggle, 1991; *S. carolinense*, Solomon, 1986, Elle, 1998; *S. campanulatum*, *S. chippendalei*, *S. clarkiae*, *S. diversiflorum*, *S. eburneum*, *S. melanospermum*, Anderson and Symon, 1989; *S. melongena*, Smith, 1931; and *S. marginatum*, Dulberger et al., 1981). Similarly, among andromonoecious species from other taxa, hermaphroditic flowers typically are larger (or heavier) than staminate flowers (*Leptospermum*, Primack and Lloyd, 1980; *Aquilegia*, Brunet, 1990; *Zigadenus*, Emms, 1993; *Anthriscus*, Spalik and Woodell, 1994; *Gagea*, Wolfe, 1998). Though not universal (exceptions include *Solanum torvum*, Hossain, 1973, *Besleria triflora*, Podolsky, 1993; and *Sagittaria guyanensis*, Huang, 2003), there appears to be a trend for larger hermaphroditic (compared to staminate) flower size among andromonoecious species.

The near ubiquity of this apparent size dimorphism among andromonoecious taxa has generated speculation about its functional and perhaps adaptive significance. For example, Anderson and Symon (1989) suggest that the larger corollas of hermaphroditic flowers promote cross-pollination of self-compatible species of *Solanum*. Conversely, smaller staminate flowers may represent a substantial resource savings that can be invested in subsequent flower production, or vegetative growth and maintenance (Bertin, 1982; Solomon, 1986).

In many *Solanum*, as well as other andromonoecious taxa, however, hermaphroditic and staminate flowers are produced in different positions within inflorescences. We show for six species of *Solanum* that when variation due to architecture is controlled, no differences in corolla characters remain (with one exception petal width in *S. candidum*). Therefore, before hypotheses for the potential functional significance of floral sexual dimorphism can be considered, the confounding effects of flower position should be determined.

Architectural effects and sexual dimorphism in Solanum—Comparison of hermaphroditic flowers from basal and distal positions within inflorescences of unpollinated plants reveals the presence of architectural effects for all of the morphological traits measured. These effects were more common in some species (*S. candidum*, *S. stramonifolium*, *S. ferox*, and *S. pseudolulo*), but in general all six species showed architectural variation in size of most floral structures and the pattern was consistently one of basal to distal decrease (Table 4). Thus, in the absence of the confounding effects of gender and resource competition from developing fruit (see Fig. 1), distal hermaphroditic flowers are predictably and significantly smaller than basal hermaphroditic flowers within the same inflorescence (Table 4; Fig. 3). Given that hermaphroditic and staminate flowers tend to be spatially segregated within inflorescences of *Solanum* (Solomon, 1985; Whalen and Costich, 1986; Anderson and Symon, 1989; Diggle, 1993; Miller and Diggle, 2003) the positional variation documented among hermaphroditic flowers within inflorescences suggests that much of the difference in size between hermaphroditic and staminate flowers may be due, not to the sexual phenotype of the flower, but to its location within an inflorescence.

In the three *Solanum* species for which staminate flower production is a fixed aspect of the phenotype, we could experimentally separate variation due to sexual phenotype from the confounding effects of architecture and fruiting history (Fig. 1B). When these effects are removed, differences between hermaphroditic and staminate flowers for most nongynoecial characteristics disappear. Thus, despite the apparent sexual dimorphism of petal size (Table 3), none actually exists (Table 4); staminate flowers have petals that are equal in length and width to hermaphroditic flowers at equivalent positions and resource status (Fig. 3). Similarly, there is no sexual dimorphism for anther dimensions for two of the three species. In contrast, significant differences between hermaphroditic and staminate flowers for primary female traits (ovary, style and stigma) remain after controlling for position and treatment (Table 4, Fig. 3). The gynoecia of staminate flowers are smaller than predicted based on inflorescence position alone and the two floral types are truly dimorphic for primary female sexual characters. Such morphological differences are consistent with the functional differences between the gynoecia of the two flower types (Miller and Diggle, 2003; J. S. Miller and P. K. Diggle, unpublished data).

In the plastic species, as in the fixed species, differences between hermaphroditic and staminate flowers for the majority of nongynoecial characters disappear after correcting for architectural effects (compare Tables 3 and 4). Thus, there is no dimorphism of these characters in the plastic species. For the remaining characters, petal width in *S. candidum*, anther length in *S. candidum* and *S. stramonifolium*, and gynoecial dimensions for all species, differences between the flower types remain. For these species, however, we cannot unequivocally separate the effects of plasticity from true sexual dimorphism (see Fig. 1A).

Plastic effects of fruiting history on floral morphology—For *Solanum* species with fixed expression of andromonoecy, plasticity of floral characters could be isolated (Fig. 1). In contrast to the dramatic effects of architecture, the effects of the fruiting treatment on flower size were minimal. Although fruit set is a cue that directly or indirectly elicits staminate flower production in the plastic species (Miller and Diggle, 2003) and clearly has an effect on other aspects of allocation such as flower or inflorescence number in these species, the sizes of most floral organs were surprisingly invariant with respect to fruit set treatment. Plasticity does not appear to contribute to size dimorphism in these species. Floral organ plasticity has been demonstrated in numerous hermaphroditic taxa, however (reviewed in Diggle, 1995; additional references in Cresswell et al., 2001), and should be examined further in taxa with unisexual flowers.

Architectural effects and the evaluation of hypotheses for the evolution of andromonoecy in Solanum—In all six species of *Solanum*, architectural effects on flower size mimic sexual dimorphism. Analyses of flower morphology made without regard to the confounding effects of architecture (and plasticity) showed profound size dimorphism between hermaphroditic and staminate flowers for both primary and secondary sexual characteristics. Elimination of these effects shows that it is primarily the gynoecium that differs between the flower types. Thus, analyses of the driving force for the evolution of andromonoecy in this group should concentrate specifically on the advantages to be gained by reducing gynoecial size and eliminating female function, rather than issues related to flower size such as resource costs or functional aspects of the corolla such as attraction or protection.

A long-standing hypothesis for the evolution of andromonoecy suggests that the production of hermaphroditic flowers is costly and the production of smaller staminate flowers conserves resources (Bertin, 1982; Solomon, 1986; Wolfe, 1998). However, because staminate flowers are not intrinsically smaller than hermaphroditic flowers, further development or investigation of this hypothesis for *Solanum* should focus exclusively on resource savings from producing nonfunctional gynoecia. Given the relatively large size of the ovary of staminate flowers (e.g., ovary length is 62–74% and width is 70–84% that of hermaphroditic flowers), the resource recovery may be minimal. An advantage may accrue, rather, from precluding post-anthesis female function of these flowers (Lloyd, 1980; Whalen and Costich, 1986). That is, termination of gynoecial development prior to anthesis will prevent investment in fruit that ultimately cannot be matured. When attention is refocused away from the confounding issues of flower size, hypotheses regarding resource allocation can be formulated with greater precision.

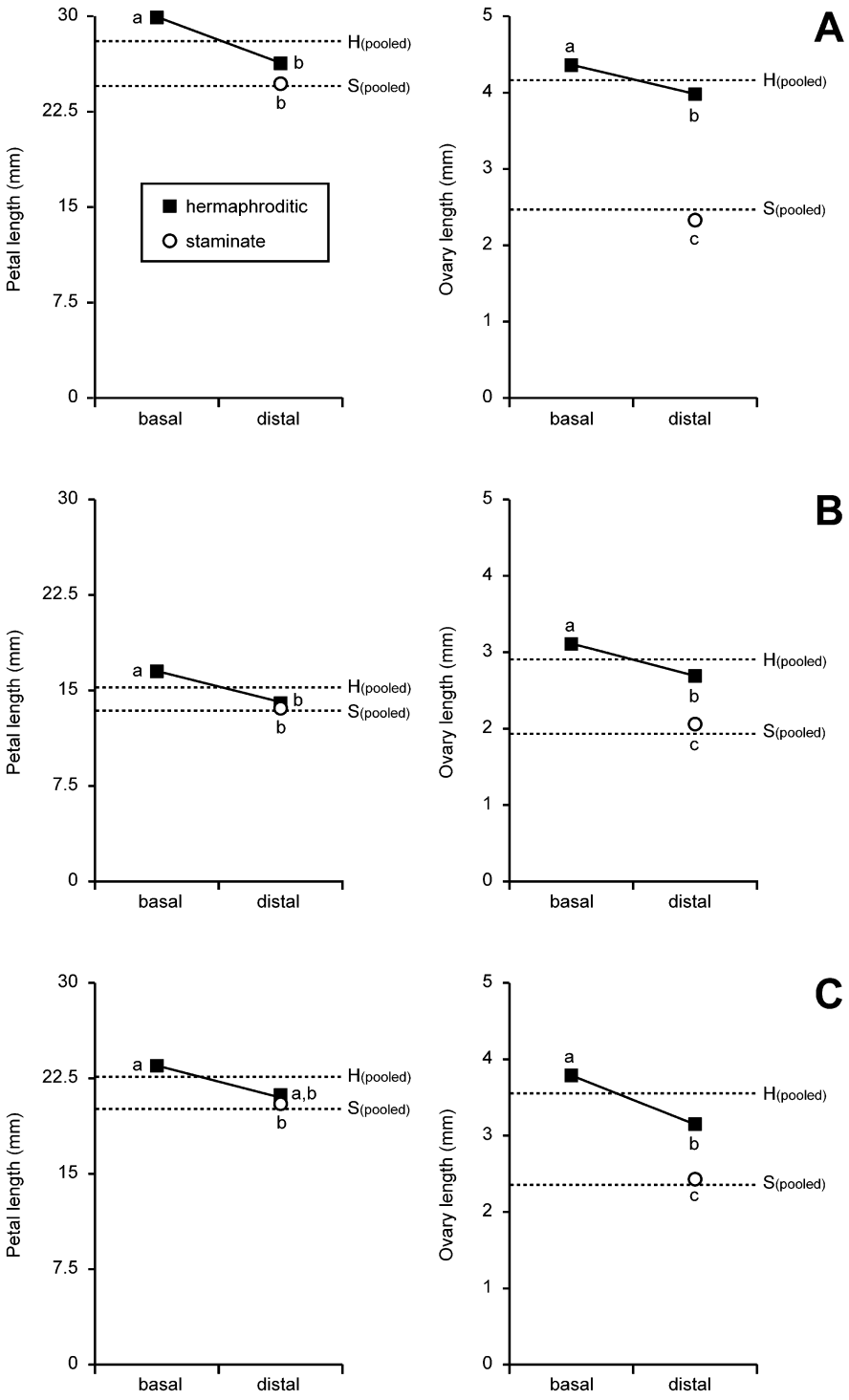

Fig. 3. Mean petal and ovary lengths for (A) *S. pectinatum*, (B) *S. pseudolulo*, and (C) *S. quitoense* as a function of flower position (basal or distal) along the inflorescence. Closed squares represent hermaphroditic flowers and open circles indicate staminate flowers of the no-fruit treatment. The dotted lines indicate the pooled hermaphroditic (H) or staminate (S) means (see Table 3). Within each figure, means associated with the same letter are not significantly different (see Table 4). These data are presented to illustrate the contributions of architecture and flower sex to differences in petal and ovary length between hermaphroditic and staminate flowers. Both organs appear to be sexually dimorphic based on pooled data. Both, however, show significant decreases with position (an architectural effect). Comparison of petal length for hermaphroditic and staminate flowers at equivalent positions shows no sexual dimorphism. In contrast, comparison of ovary lengths between distal hermaphroditic and staminate flowers shows that ovaries are significantly sexually dimorphic and are smaller in staminate flowers.

Another potential explanation for the presence of reduced gynoecia in staminate flowers may be interference of pollen export (male function) by female sexual structures (Solomon, 1985; Elle and Meagher, 2000). The general importance of interference between gender functions has received recent attention (Fetscher, 2001; Barrett, 2002) and its relevance to the evolution of andromonoecy is highlighted by focusing specifically on gynoecial differences between the flower types. In hermaphroditic flowers of *Solanum*, the style exceeds the stamens in length and protrudes from the central cone formed by five poricidal anthers. *Solanum* species are buzz-pollinated, a syndrome in which a pollen-collecting bee curls its body over the androecium and vibrates the stamens, causing the release of pollen onto the insect (Whalen, 1979, 1984). It is possible that the protruding style interferes with this process and hence, with pollen export. The production of staminate flowers with shorter styles could enhance male function via increased efficiency of pollen removal. Geitonogamous pollen discounting (Barrett, 2002) might also be reduced because the stigmas of staminate flowers would not receive pollen from previously visited flowers. Consistent with an hypothesis of interference is the occurrence of enantiostyly in the closely related *Solanum* section *Androceras* (Whalen, 1984). In enantiostylous species, such as *Solanum rostratum*, all flowers are morphologically hermaphrodite, but the style is curved to one side, does not protrude through the cone of anthers (Bowers, 1975) and does not interfere with pollen collection (Jesson and Barrett, 2002, 2003). This interference hypothesis could be experimentally tested in andromonoecious *Solanum*.

Summary—The discovery of significant architectural variation that mimics floral sexual dimorphism across several species of *Solanum* leads us to question how many other reports of size dimorphism reported in the literature may, in fact, be due to architectural differences. This is an empirical question and requires analysis of the extent to which unisexual flowers are produced in distinct locations within the architecture of inflorescences or individuals. Information about the spatial distribution of unisexual flower in diverse taxa is not readily available but consideration of a few examples suggests that further analysis is warranted. A survey of andromonoecious taxa shows that hermaphroditic and staminate flowers are almost universally segregated within or among inflorescences (Bell, 1971; Hopkins, 1984; Solomon, 1985; Diggle, 1993; Hoc et al., 1994; Ladd, 1994; Emms et al., 1997; Elle, 1998; Krupnick and Weiss, 1998; Manicacci and Despres, 2001; Miller and Diggle, 2003). Monoecious species may have female and male flowers segregated within inflorescences (Matzke, 1938; Willson and Ruppel, 1984; Cox, 1988), as in andromonoecy, or the two flower types may occur on inflorescences that differ dramatically in location or morphology (Jones, 1936; Bell, 1971; Abul-Fatih and Bazzaz, 1979; Lovett Doust, 1980; Condon and Gilbert, 1988; Delasalle, 1992; Costich, 1995). Dioecious taxa also may have gender specific inflorescence morphology (Whitiker and Davis, 1962; Bawa, 1980; Costich, 1995). If patterns of spatial segregation of flower types such as these are common among taxa with unisexual flowers, then the confounding effects of architecture may be creating patterns of sexual dimorphism where no inherent difference in the flower types exist. Thus, we propose that consideration of architectural effects on flower size is a critical component of analyses of unisexual flowers and should precede the evaluation of evolutionary hypotheses regarding form and function.

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