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CORRELATED EVOLUTION OF FRUIT SIZE AND SEXUAL EXPRESSION IN ANDROMONOECIOUS *SOLANUM* SECTIONS *ACANTHOPHORA* AND *LASIOCARPA* (SOLANACEAE)[1]

JILL S. MILLER[2,5] AND PAMELA K. DIGGLE[3,4,5]

[2]Department of Biology, Amherst College, Amherst, Massachusetts 01002 USA; and
[3]Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, Colorado 80309 USA

Andromonoecy is hypothesized to evolve as a mechanism enabling plants to independently allocate resources to female and male function. If staminate flower production is a mechanism to regulate allocation to female function (i.e., fruit production), then large-fruited species should be more strongly andromonoecious than smaller-fruited taxa because more resources are required to mature large fruit. We combined phylogenetically independent contrast analyses with extensive phenotypic characterization under common greenhouse conditions to examine the predicted relationship between fruit mass and the strength of andromonoecy among 13 species in *Solanum* sections *Acanthophora* and *Lasiocarpa*. The strength of andromonoecy, defined as the proportion of staminate flowers produced within inflorescences, was significantly and positively associated with fruit mass in both naïve and phylogenetically independent analyses. Our results are consistent with the hypothesis that andromonoecy functions as a mechanism to regulate allocation to female function and suggest that the strength of andromonoecy is also associated with resource limitation. In general, we find that strong andromonoecy appears to arise via reductions in hermaphroditic flower number. However, increases in staminate flowers have also contributed to transitions to strong andromonoecy in certain species. Finally, our analyses identified a suite of correlated characters (flower size, ovary width, fruit mass) that are associated with changes in the sexual expression of andromonoecy.

Key words: *Acanthophora*; andromonoecy; CAIC; flower size; fruit mass; fruit size; independent contrasts; *Lasiocarpa*; PDAP; phylogeny; Solanaceae; *Solanum*.

Andromonoecy is a sexual system in which plants produce both hermaphroditic and female-sterile (staminate) flowers. Although the number of andromonoecious angiosperm species is relatively modest (approximately 4000 [Yampolsky and Yampolsky, 1922]), these species are nested in at least 33 families (Yampolsky and Yampolsky, 1922; Miller and Diggle, 2003). This distribution suggests numerous independent origins of andromonoecy, and considerable attention has focused on identifying the conditions under which this sexual system has evolved and diversified (e.g., Bertin, 1982; Whalen and Costich, 1986; Anderson and Symon, 1989; Spalik, 1991; Diggle, 1993, 1994; Podolsky, 1993; Emms, 1996; Emms et al., 1997; Elle and Meagher, 2000; Miller and Diggle, 2003; Vallejo-Marín and Rausher, 2007).

A common theme in discussions of the evolution of andromonoecy is the suggestion that production of both hermaphroditic and staminate flowers allows resource allocation to female and male reproductive function to be flexible (Lloyd, 1980; Bertin, 1982; Solomon, 1985; Sutherland, 1986; Diggle, 1994; Miller and Diggle, 2003). Consistent with this idea, andromonoecy is often associated with resource limitation of fruit set and with individual fruits that are large and costly (see summary in Bertin, 1982; Lloyd, 1979; Primack and Lloyd, 1980; Lloyd and Bawa, 1984; Sutherland, 1986; Whalen and Costich, 1986; May and Spears, 1988; Spalik, 1991; Diggle, 1993, 1994; Emms, 1996). Termination of gynoecial development before anthesis and the resulting production of a morphologically staminate flower prevent allocation to a fruit that cannot mature while maintaining potential male function (Ruiz Zapata and Kalin Arroyo, 1978; Solomon, 1986; Sutherland, 1986; Spalik, 1991).

Although these resource allocation hypotheses address the selective advantages that may drive the evolutionary origin of andromonoecy, they have not been used to explain subsequent evolutionary diversification in the degree of andromonoecy observed among species. Because of the modular nature of flower production, the expression of andromonoecy varies quantitatively; that is, individuals and species exist along a continuum from weakly andromonoecious (i.e., producing a small proportion of staminate flowers per inflorescence) to strongly andromonoecious (i.e., producing a large proportion of staminate flowers per inflorescence).

Andromonoecy is particularly common and variable in strength among members of the genus *Solanum* subgenus *Leptostemonum*. Whalen and Costich (1986) proposed that variation in sexual expression among these species should be directly related to fruit size. They reasoned that if, as is commonly hypothesized, the production of staminate flowers via suppression of gynoecial development is a mechanism to control fruit initiation, then larger-fruited species should be more strongly andromonoecious than smaller-fruited species. Their analysis of fruit diameter and the strength of andromonoecy showed a strong correlation for members of *Solanum* sections *Lasiocarpa* and *Acanthophora*.

This correlation, however, was based on limited sampling

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[4] Author for correspondence (e-mail: pamela.diggle@colorado.edu)

[5] Authors contributed equally to this research.

TABLE 1. Species means of floral and fruit traits for 13 species in *Solanum* sections *Acanthophora* and *Lasiocarpa*. Values for the proportion of staminate flowers are back-transformed means. The first principal component (PC1) from an analysis of eight floral characters is an index of flower size. S = staminate, H = hermaphroditic.

Species and section	Proportion S flowers	Fruit mass (g)	Fruit no.	No. flowers	No. H flowers	No. S flowers	PC1	Ovary width (mm)
Section *Acanthophora*								
S. acerifolium	0.062	—	—	4.7	3.8	0.9	—	—
S. capsicoides	0.092	0.44	3.2	5.6	4.4	1.1	−3.535	2.05
S. mammosum	0.642	5.60	0.9	6.7	2.4	4.3	0.995	3.09
S. palinacanthum	0.908	2.08	0.5	6.6	1.1	5.5	0.788	2.98
S. tenuispinum	0.001	0.33	9.0	11.2	11.2	0.1	−2.707	1.75
Section *Lasiocarpa*								
S. candidum	0.146	1.53	2.1	8.3	6.5	1.8	−1.573	3.09
S. lasiocarpum	0.205	1.29	2.6	5.5	4.1	1.4	−0.667	2.98
S. repandum	0.150	7.34	1.3	4.1	3.2	0.9	0.591	3.84
S. hirtum	0.187	1.42	2.8	5.6	4.1	1.5	0.249	3.24
S. pectinatum	0.785	3.67	0.4	2.6	0.7	1.9	3.556	3.71
S. pseudolulo	0.402	1.64	0.7	4.7	2.6	2.1	−1.160	3.56
S. quitoense	0.660	5.71	0.9	9.5	3.1	6.4	2.807	5.51
S. stramoniifolium	0.103	0.70	7.7	16.5	14.0	2.5	−2.494	2.54

within species and did not control for nonindependence of species due to common ancestry. Because traits like fruit size and sexual expression may be correlated with phylogeny, a more powerful test of the association should consider shared evolutionary history among these taxa. Further, it is not clear from this analysis how andromonoecy is actually related to fruit size. Because the strength of andromonoecy is expressed as a proportion of flower types, the observed correlation could be due to evolutionary changes in hermaphroditic or staminate flower number, or both. Moreover, changes in the proportion of flower types must occur within the context of total flower production, yet it is unknown whether changes in the strength of andromonoecy are necessarily associated with increases or decreases in flower number (Whalen and Costich, 1986; Anderson and Symon, 1989). Fruit size is also likely to be developmentally related to the size of the ovary from which the fruit develops (Primack, 1987; Gillaspy et al., 1993; Frary et al., 2000), and ovary size, in turn, may be correlated to the sizes of other floral organs (Elle, 1998; Ashman and Majetic, 2006). Thus, evolutionary changes in fruit size may be correlated with changes in both ovary and flower size, and these may also show a relationship with evolutionary change in the strength of andromonoecy.

The relationship among the strength of andromonoecy and associated floral and fruit characters can be examined with comparative data coupled with phylogenetic hypotheses for relationships among species. The closely related members of *Solanum* sections *Lasiocarpa* and *Acanthophora* vary extensively in the expression of andromonoecy. Staminate flower production varies among species from near zero to 90% of flowers per inflorescence (Diggle, 1993; Miller and Diggle, 2003) (Table 1). In addition, hypotheses of evolutionary relationships for these groups are available (Bruneau et al., 1995; Bohs, 2004; Levin et al., 2006), and the monophyly of sections *Lasiocarpa* (Bohs, 2004) and *Acanthophora* sensu stricto (Levin et al., 2005), as well as the sister relationship between the two clades, is well supported (Bohs, 2004; Levin et al., 2005).

We used phylogenetically independent contrasts and character reconstruction to examine factors that might underlie a relationship between evolutionary changes in fruit size and variation in the strength of andromonoecy in *Solanum* sections *Lasiocarpa* and *Acanthophora*. Specifically we asked whether variation among species in fruit mass is correlated with the strength of andromonoecy. We also investigated the contribution of the absolute numbers of hermaphroditic, staminate, and total flowers per inflorescence to evolutionary changes in the proportion of flower types produced. Finally, we explored the possibility that the relationship between evolutionary changes in the strength of andromonoecy and fruit size also involves a larger suite of floral characters, including ovary and flower size.

MATERIALS AND METHODS

Study species—Section *Lasiocarpa* is a small (12 species) monophyletic section within the spiny *Solanum* group (subgenus *Leptostemonum*; Bohs, 2004; Levin et al., 2006). Most of the species occur in northwestern South America, although two species are found in Asia and the Pacific Islands. As originally circumscribed (Nee, 1979), the approximately 20 species in section *Acanthophora* (also in subgenus *Leptostemonum*) are not monophyletic; however, the majority of species traditionally classified in this section and included to date in phylogenetic analyses (Levin et al., 2005, 2006) are in a strongly supported monophyletic group (see Levin et al., 2006) that includes the five species of *Acanthophora* reported on here. Further, there is strong support for a sister relationship between sections *Lasiocarpa* and *Acanthophora* (Levin et al., 2005, 2006). Species of both sections are all sexually reproducing, self-compatible, and andromonoecious (Nee, 1979; Whalen et al., 1981).

All species were cultivated in greenhouses at the University of Colorado (Boulder, Colorado, USA). The study included 13 species: eight of 12 species in section *Lasiocarpa*, including *Solanum candidum*, *S. lasiocarpum*, *S. repandum*, *S. hirtum*, *S. pectinatum*, *S. pseudolulo*, *S. quitoense*, and *S. stramoniifolium*; and five of the 19 species in the Acanthophora clade (as defined in Levin et al., 2006), including *S. acerifolium*, *S. capsicoides*, *S. mammosum*, *S. palinacanthum*, and *S. tenuispinum*.

Cultivation of plants and data collection—Plants were grown from seed, and 5–12 genotypes for each species were clonally replicated via vegetative cuttings to produce genetically identical replicates. Each clonal replicate was transplanted into an 11-L pot containing a 2 : 1 mix of Fafard Growing Mix #2 (Conrad Fafard, Agawam, Massachusetts, USA) to Persolite (Persolite Products, Florence, Colorado, USA) plus Osmocote 13-13-13 slow-release fertilizer (Scotts, Marysville, Ohio, USA). Plants were watered daily with 150–200 ppm of Excel Magnitrate fertilizer (Scotts).

Clonal replicates for each genotype were randomly assigned positions in the greenhouses. We pollinated all open hermaphroditic flowers every other day using a mixture of pollen collected from several (three or more genotypes) conspecific pollen donors. Hermaphroditic flowers remained open for 2 to 3 d, and most flowers were pollinated at least twice.

Two branches on each plant were selected and censused every other day. Early developing, basal inflorescences were numbered first, and floral positions within inflorescences were also numbered from the base to the tip. Inflorescence position, flower position, floral sexual phenotype (i.e., hermaphrodite or staminate), and fruit production were recorded for all flowers on up to 10 inflorescences on each of two marked branches per individual. Data were summarized initially for each inflorescence position on each genotype for each species. We then calculated the average number of hermaphroditic, staminate, and total flowers per inflorescence, as well as the average number of fruits per inflorescence for each species. The strength of andromonoecy was expressed as the proportion of staminate flowers produced within inflorescences. Proportions were arcsine-square-root transformed (Sokal and Rohlf, 1995) prior to analyses and were back transformed for presentation.

All fruits produced on marked branches were collected, dried completely at 60°C, and weighed to the nearest milligram on a XL-400D balance (Denver Instruments, Denver, Colorado, USA). In total, 7310 fruit were weighed across 12 (excluding *S. acerifolium*) species (range 28–2197 fruits per species), and average fruit mass for inflorescence, genotype, and species combinations was calculated. Fruit mass was multiplied by 100 and log transformed prior to analyses.

Flowers from uncensused branches were collected for floral measurements. Because floral position within an inflorescence strongly affects the size of structures (Diggle and Miller, 2004), we used only hermaphroditic flowers produced in basal positions within inflorescences. Recently opened flowers (<48 h old) were collected and fixed in FAA (formalin-acetic acid-alcohol; Berlyn and Miksche, 1976) for 24 h before transfer to 70% ethanol for storage. Flowers were measured using digital calipers (for large corollas) and a Zeiss (Thornwood, New York, USA) Stemi SV-11 dissecting microscope equipped with a Zeiss Axiophot digital camera and image analysis system. For each flower, eight measurements were made: length and width of the dorsal petal, anther length and width, style length, stigma width, and ovary length and width. Principal component analysis was used to summarize variation in the floral characters (JMP version 5.0.1, SAS Institute, 1989–2002). The first principal component was used as an index of flower size in the contrast analyses. In total, we measured 585 flowers collected from 101 genotypes from 12 species (all except *S. acerifolium*). We measured 5.8 flowers, on average, from within genotypes and included an average of 8.4 genotypes for each species. All floral measurements were log transformed prior to analyses.

Interspecific correlations—Interspecific correlations among characters were calculated as Pearson product–moment correlations using the species means for each of the characters. Data summaries and correlation analyses were done in JMP version 5.0.1 (SAS Institute, 1989–2002).

Phylogenetic hypotheses and independent contrasts—Several hypotheses of evolutionary relationships were used to conduct independent contrasts analyses. First, we used results from Bohs (2004), who analyzed chloroplast-sequence data from the *trnT-trnL* and *trnL-trnF* spacers and the *trnL* gene to infer relationships within section *Lasiocarpa*. That study also included the five members of section *Acanthophora* studied here. We used relationships depicted in Fig. 1 of Bohs (2004) with one modification. In that topology, two accessions of *S. repandum* were not monophyletic, and here we used two trees, each depicting one of the positions for this taxon (topologies IA and IB in Fig. 1).

We also used results from Levin et al. (2006), who inferred relationships among a larger set of taxa in *Solanum* subgenus *Leptostemonum* using a combined analysis of the nuclear internal transcribed spacer region, the granule-bound starch synthase gene, and the chloroplast spacer region *trnS-trnG*. Specifically, we used the topology from their Bayesian analysis of combined data (Fig. 3 in Levin et al., 2006). There is one polytomy in this tree and weak support for the node uniting *S. hirtum* and *S. pseudolulo* (see topology II, Fig. 1); we reconciled the polytomy and relationships among *S. hirtum*, *S. pseudolulo*, and *S. pectinatum* in all possible ways and used these topologies (topologies IIA1–IIA3, IIB1–IIB3, and IIC1–IIC3 in Fig. 1) in independent contrasts.

Finally, we obtained sequence data for the *trnS-trnG*, *trnT-trnF*, ITS, and *waxy* regions from the authors of the published sources (Bohs, 2004; Levin et al., 2005, 2006) and aligned these regions manually using SeAl (Rambaut, 2002). Phylogenetic analysis of sequence data was carried out using maximum likelihood as implemented in PAUP* version 4.0b10 (Swofford, 2002). Maximum likelihood model parameters were determined using the Akaike information criterion in Modeltest v. 3.7 (Posada and Crandall, 1998). The best model (GTR+I+G) was used in a likelihood analysis in PAUP* using the heuristic search option, eight starting trees from a parsimony analysis, tree-bisection-reconnection (TBR) branch swapping, and the MulTrees option in effect. The five species in section *Acanthophora* were designated as outgroups in this analysis. We used the most likely tree from this analysis in independent contrasts (topology III in Fig. 1).

Phylogenetically independent contrasts were conducted for each of the 13 topologies depicted in Fig. 1 using the PDAP module version 1.07 (Midford et al., 2003) in Mesquite version 1.06 (Maddison and Maddison, 2005). All branch lengths were set to one (Diaz-Uriarte and Garland, 1998). Diagnostic tests in PDAP were run to ensure that the contrasts were properly standardized (Garland et al., 1992; Purvis and Rambaut, 1995; Freckleton, 2000). We tested the relationship between variables by least-squares linear regressions of the contrasts forced through the origin (Harvey and Pagel, 1991; Garland et al., 1992). Significant contrast correlations would support the hypothesis that evolutionary change in one character is consistently related (positively or negatively) to change in the second character across the clade.

Correlations between the strength of andromonoecy, defined as the proportion of staminate flowers produced within inflorescences, and the variables that make up that proportion (staminate, hermaphroditic, and total flower number) are inherently interrelated. We therefore explored the relationship of the strength of andromonoecy and changes in flower number using two alternative approaches. First, we used the BRUNCH procedure of the program CAIC (Purvis and Rambaut, 1995) to examine correlated changes in a categorical variable and a continuous variable. Species were categorized as having either weak andromonoecy (20% or fewer staminate flowers within inflorescences) or strong andromonoecy (40% or higher staminate flowers within inflorescences), and we tested whether the evolution of continuous variables (total, hermaphroditic, or staminate flower production) is associated with the evolution of the categorical variable (weak vs. strong andromonoecy). Positive contrasts for the strength of andromonoecy would indicate that the continuous variable changed in the same direction as the categorical variable, whereas negative contrasts would indicate that the continuous variable changed in the opposite direction as the categorical variable.

In addition, we reconstructed the evolutionary shifts in flower number across the transition from weak to strong andromonoecy for selected taxa. *Solanum quitoense* and *S. pectinatum* are both strongly andromonoecious, yet they differ dramatically in both total flower production and the numbers of hermaphroditic and staminate flowers (Table 1). Whereas *S. quitoense* produces numerous flowers within inflorescences and many of these are staminate, *S. pectinatum* typically bears 2–3 flowered inflorescences with only a single hermaphroditic flower in each. Values for total, hermaphroditic, and staminate flower number were inferred for ancestral species using squared-change parsimony as implemented in Mesquite version 1.06 (Maddison and Maddison, 2005). We calculated the change in flower number from the ancestor leading to *S. quitoense* and *S. pectinatum* to explore the evolutionary transitions of flower number associated with strong andromonoecy in each of these taxa. Reconstructions were repeated for all topologies as a test of the sensitivity of our inferences to uncertainty in phylogeny.

RESULTS

Species means for the strength of andromonoecy (proportion staminate flowers); fruit mass and number; total-, hermaphroditic-, and staminate-flower production; ovary width; and the first principal component are in Table 1. There was considerable variation among species for these characters. For example, fruit dry mass varied among species by more than an order of magnitude, from 0.33 to 7.34 g, and similarly the proportion of staminate flowers per inflorescence ranged from nearly zero to just over 0.90. The first principal component (PC1) accounted for 59% of the total variation in the data set and described overall flower size. The eigenvector associated with PC1 had positive loadings for all the floral characters, and these loadings were of similar magnitude, characteristic of a size vector.

Fruit mass, fruit number, and the strength of andromonoecy—As fruits got larger, the strength of andromonoecy increased among the *Solanum* species included in the

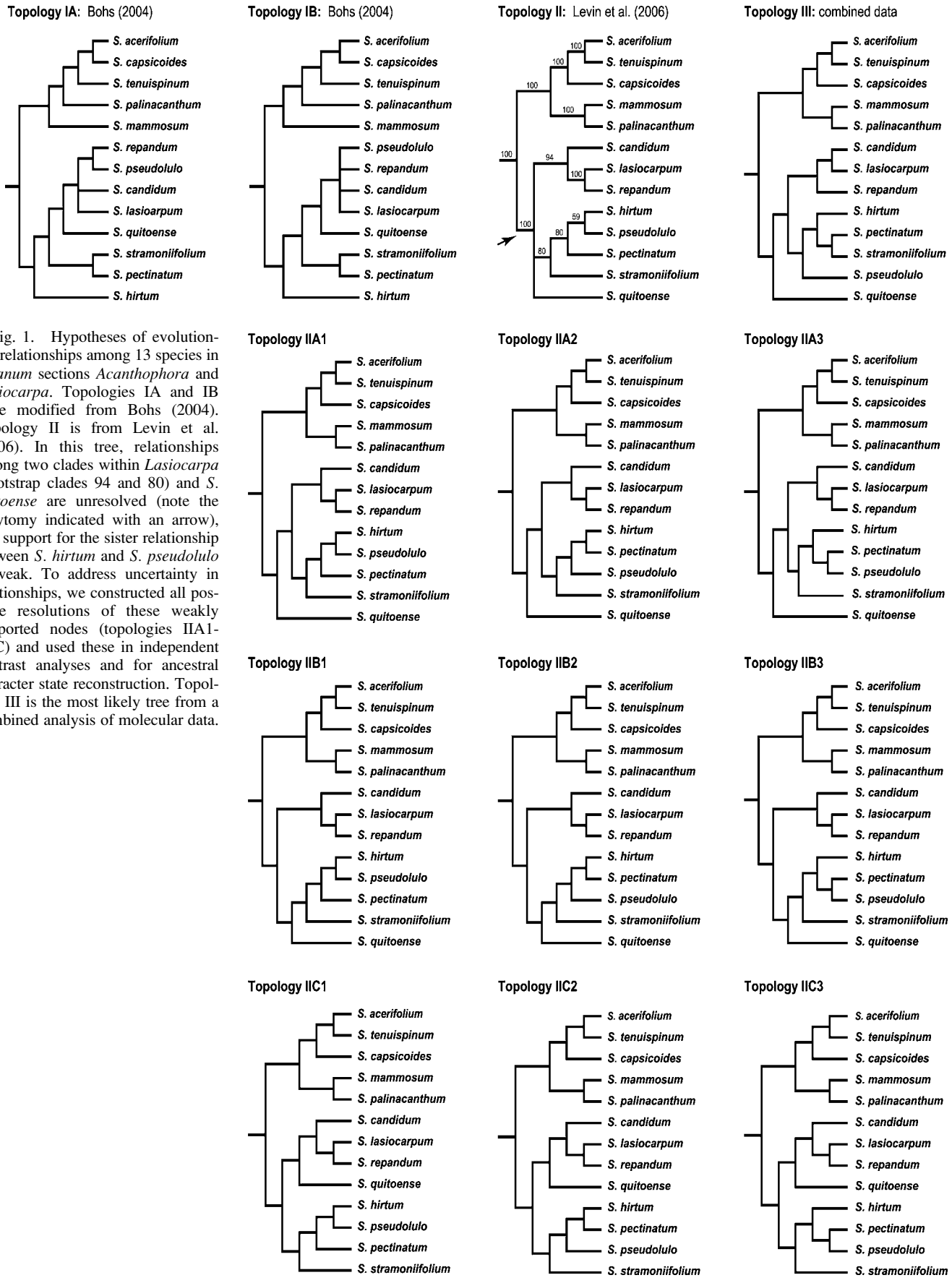

Fig. 1. Hypotheses of evolutionary relationships among 13 species in *Solanum* sections *Acanthophora* and *Lasiocarpa*. Topologies IA and IB were modified from Bohs (2004). Topology II is from Levin et al. (2006). In this tree, relationships among two clades within *Lasiocarpa* (bootstrap clades 94 and 80) and *S. quitoense* are unresolved (note the polytomy indicated with an arrow), and support for the sister relationship between *S. hirtum* and *S. pseudolulo* is weak. To address uncertainty in relationships, we constructed all possible resolutions of these weakly supported nodes (topologies IIA1-II3C) and used these in independent contrast analyses and for ancestral character state reconstruction. Topology III is the most likely tree from a combined analysis of molecular data.

TABLE 2. Interspecies and phylogenetically independent contrast correlations between fruit mass and the strength of andromonoecy and fruit mass and fruit number. Significance of the correlations are in parentheses. Independent contrasts were carried out on multiple topologies to incorporate phylogenetic uncertainty (see Materials and Methods and Fig. 1).

	Fruit mass	
Analysis	Andromonoecy	Fruit number
Interspecies	0.65 (0.022)	−0.76 (0.004)
Independent contrasts		
IA	0.66 (0.019)	−0.72 (0.008)
IB	0.65 (0.022)	−0.72 (0.008)
II	0.59 (0.045)	−0.67 (0.016)
IIA1	0.57 (0.054)	−0.66 (0.019)
IIA2	0.55 (0.061)	−0.65 (0.022)
IIA3	0.54 (0.069)	−0.62 (0.031)
IIB1	0.58 (0.048)	−0.68 (0.015)
IIB2	0.59 (0.043)	−0.68 (0.015)
IIB3	0.58 (0.047)	−0.65 (0.021)
IIC1	0.58 (0.046)	−0.66 (0.020)
IIC2	0.59 (0.043)	−0.65 (0.022)
IIC3	0.58 (0.048)	−0.62 (0.031)
III	0.59 (0.042)	−0.67 (0.016)

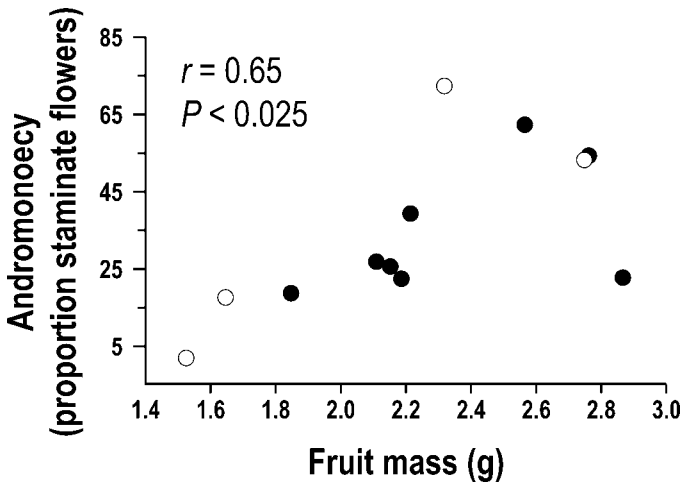

Fig. 2. Interspecies correlation of fruit mass and the strength of andromonoecy among species of *Solanum* in sections *Acanthophora* (open circles) and *Lasiocarpa* (closed circles). Values on the *y*-axis are arcsine-square-root transformed proportions, and values on the *x*-axis are multiplied by 100 and log transformed. The Pearson product moment correlation (r) and significance (P) are given.

interspecific analysis (Pearson product moment correlation, $r = 0.65$, $P = 0.022$; Table 2; Fig. 2). Further, this relationship persisted after accounting for evolutionary history using independent contrasts. Contrast correlations involving fruit mass and the strength of andromonoecy were positive and significant ($0.58 \leq r \leq 0.66$, $P \leq 0.05$; Table 2) for all but three topologies in which *S. quitoense* is basal within *Lasiocarpa* (topologies IIA1–IIA3, see Fig. 1). The relationship was marginally significant even for these topologies ($0.54 \leq r \leq 0.57$, $0.05 < P \leq 0.07$; Table 2).

There was a trade off between fruit mass and fruit number for interspecies correlations ($r = -0.76$, $P = 0.004$; Table 2), and this relationship also persisted in independent contrasts. Contrast correlations were significant across all topologies ($-0.72 \leq r \leq -0.62$, $0.008 \leq P \leq 0.031$; Table 2).

Flower number and the strength of andromonoecy—Interspecies correlations of the strength of andromonoecy and total, hermaphroditic, and staminate flower numbers are inherently interrelated because the latter are used to calculate the strength of andromonoecy. Of the variables used to calculate the strength of andromonoecy, hermaphroditic flower number was negatively associated with fruit mass ($r = -0.66$, $P = 0.02$), but no relationship was detected between fruit mass and either total ($r = -0.43$, $P = 0.16$) or staminate ($r = 0.52$, $P = 0.08$) flower number. This pattern remained following contrast correlations; hermaphroditic flower number was negatively related to fruit mass for all topologies ($-0.67 \leq r \leq -0.58$, $P \leq 0.05$), whereas correlations of fruit mass with either total or staminate flower number were not significant for any topology.

We also investigated the relationship between the strength of andromonoecy and flower production by analyzing the strength of andromonoecy as a categorical variable. Because of small sample sizes (i.e., three to five transitions between weak and strong andromonoecy within topologies), testing for significance was limited. Despite this limitation, results of the categorical analysis were similar to those contrasts based on the continuous variables described in the previous paragraph. No relationship of andromonoecy to total or staminate flower production was detected, whereas contrasts for hermaphroditic flower number were negative for all topologies and significant for four of these (topologies IIA2–3 and IIB2–B3; $13.5 \leq F \leq 221.9$, $0.005 \leq P \leq 0.035$).

Finally, we examined evolutionary transitions in flower number using ancestral character state reconstructions. We focused on the species *S. quitoense* and *S. pectinatum*, because these taxa differ widely in total flower number per inflorescence (9.5 and 2.6, respectively; Table 1) while sharing strong andromonoecy (Table 1). Figure 3 shows the change in hermaphroditic and staminate flower number from the relevant ancestral species to *S. quitoense* and *S. pectinatum*. Hermaphroditic flower number decreased for both species in all topologies (Fig. 3) and significantly more so for some topologies in *S. pectinatum*. In contrast, staminate flower number remained relatively unchanged in *S. pectinatum*, whereas staminate flower number increased in *S. quitoense*.

Relationships among fruit mass and floral characters—Fruit mass was positively associated with ovary width ($r = 0.86$, $P = 0.0004$; Fig. 4A) and flower size ($r = 0.84$, $P = 0.0006$; Fig. 4B), and ovary width and flower size were also correlated ($r = 0.80$, $P = 0.0017$; Fig. 4C). These relationships remain following independent contrasts for all topologies (ovary width and fruit mass, $0.83 \leq r \leq 0.86$, $P \leq 0.0008$; flower size and fruit mass, $0.77 \leq r \leq 0.85$, $P \leq 0.003$; flower size and ovary width, $0.68 \leq r \leq 0.84$, $P \leq 0.015$). In addition to being correlated with one another, ovary width and flower size were also significantly correlated with the strength of andromonoecy in both interspecific (Fig. 4D, E) and independent contrast analyses (ovary width and andromonoecy, $0.61 \leq r \leq 0.76$, $P \leq 0.04$; flower size and andromonoecy, $0.75 \leq r \leq 0.80$, $P \leq 0.005$).

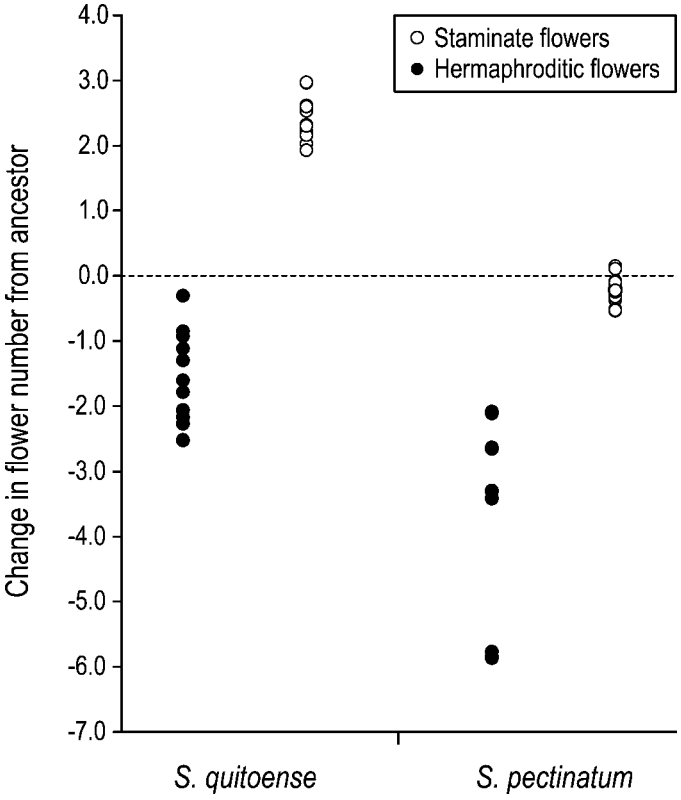

Fig. 3. The change in hermaphroditic (closed circles) and staminate (open symbols) flower number from the respective ancestors leading to *Solanum quitoense* and *S. pectinatum* for the thirteen topologies in Fig. 1. The dashed line indicates no change from the ancestral species, whereas increases and decreases in flower number are above and below the line, respectively.

DISCUSSION

Andromonoecy is thought to evolve as a mechanism that curtails allocation to female function within some flowers without altering male function (reviewed in Bertin, 1982; Diggle, 1994). Whalen and Costich (1986) extended this independent allocation hypothesis in an attempt to explain the broad variation in the strength of andromonoecy observed among *Solanum* species. They reasoned that if staminate flower production is a mechanism to regulate allocation to female function (fruit production), then large-fruited species should be more strongly andromonoecious than smaller-fruited taxa because more resources are required to mature large fruit. Our investigation combined phylogenetically independent contrasts with extensive phenotypic characterization to exam-

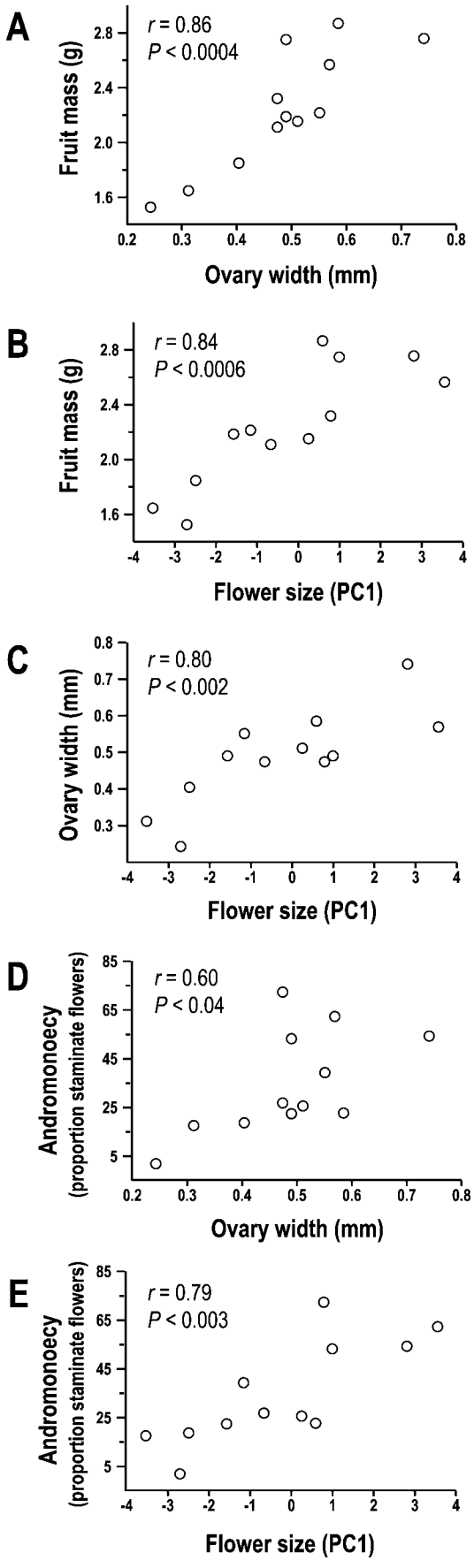

Fig. 4. Interspecies correlations for fruit and floral traits among 13 species of *Solanum*. Pearson product moment correlations (r) and significance (P) are indicated. Panels A–C depict correlations among fruit mass, flower size (PC1), and ovary width, and panels D and E show correlations of ovary width and flower size (PC1) with the strength of andromonoecy. Values on the y-axis of panels D and E are arcsine-square-root transformed proportions, ovary width is log transformed (panels A, C, D), and fruit mass is multiplied by 100 and log transformed (panels A and B).

ine the predicted relationship between fruit mass and the strength of andromonoecy in *Solanum*. We confirmed this prediction and showed that the correlation between fruit size and the strength of andromonoecy is due largely to an underlying association between evolutionary changes in fruit mass and hermaphroditic flower number. Moreover, fruit mass, ovary size, and flower size comprise a suite of characters that evolve with changes in the expression of andromonoecy.

Evolution of fruit size and the strength of andromonoecy—As predicted (Whalen and Costich, 1986), the interspecific correlation of fruit mass and the strength of andromonoecy is positive and significant (Table 2; Fig. 2). More importantly, this relationship persists after accounting for shared evolutionary history and is generally robust to uncertainty in evolutionary relationships (Table 2; Fig. 1). Many of the contrast correlation coefficients are very close to the interspecific values, suggesting that there is little phylogenetic constraint on these characters (Armbruster et al., 2002). Fruit characteristics are sometimes considered to be evolutionarily conservative (Spujt, 1994; Knapp, 2003), yet within this small group of *Solanum*, fruit size is apparently quite labile. The ecology of frugivory and fruit dispersal in relation to fruit size in this group merits investigation.

Both interspecific and independent contrast correlations confirm that, within the clade containing *Solanum* sections *Acanthophora* and *Lasiocarpa*, evolutionary changes in the strength of andromonoecy generally are positively associated with changes in fruit size. Particular contrasts, however, are not consistent with this pattern. The contrast between *S. repandum* and *S. pseudolulo* in topology IA (Fig. 1) and the contrast of and *S. mammosum* and *S. palinacanthum* in many topologies (topologies, II–III; Fig. 1) represent cases in which weaker andromonoecy is associated with larger fruit. The species pair, *S. mammosum* and *S. palinacanthum*, both have strong andromonoecy (>60% staminate flower production within inflorescences; Table 1) and the largest fruits of any *Acanthophora* (Levin et al., 2005). Because the sister relationship of these species is strongly supported in most topologies (Fig. 1) and also in a more comprehensive phylogenetic investigation of section *Acanthophora* (Levin et al., 2005), it is likely that the evolution of both large fruits and strong andromonoecy occurred in the common ancestor of these taxa. Subsequent evolution of fruit of these species, however, is likely related to other aspects of their reproductive biology. For example, *S. mammosum* produces very unusual, elongated fruits that are subtended by supernumerary carpels (termed mammillae; Miller, 1969). Despite the presence of large fruit and relatively weak andromonoecy in *S. mammosum* (as compared with *S. palinacanthum*), within each species, the genotype means of the strength of andromonoecy and of fruit mass are positively correlated (*S. mammosum*, $N = 12$ genotypes, $r = 0.70$, $P = 0.011$; *S. palinacanthum*, $N = 8$ genotypes, $r = 0.82$, $P = 0.013$). Thus, for both species, genotypes with large fruit are more strongly andromonoecious, a result consistent with the general relationship observed among species of *Lasiocarpa* and *Acanthophora*.

The prediction that strong andromonoecy is associated with large fruit (Whalen and Costich, 1986) assumes that resources limit fruit production. Our data indicate trade-offs between fruit size and number for both interspecific and independent contrast analyses (Table 2); among the species studied, evolutionary changes in fruit size generally have been accompanied by inverse changes in fruit number. Such trade-offs between fruit size and number are common among fleshy-fruited taxa and are often attributed to resource competition and reallocation within inflorescences (Veliath and Ferguson, 1972; Stephenson, 1981; Wyatt, 1982; Diggle, 1995; Elle, 1996; Lee, 1988; Nesbitt and Tanksley, 2001; Baldet et al., 2006). It is unknown whether the among-species variation in fruit number seen here (Table 1) is a direct consequence of changes in fruit size (and resultant changes in resource competition within inflorescences) or whether separate regulation of fruit number also has evolved.

Flower number and the strength of andromonoecy—The relationship between evolutionary changes in fruit size and changes in the strength of andromonoecy must be due to an underlying correlation of fruit mass with the individual elements used to calculate the strength of andromonoecy: staminate flower number, hermaphroditic flower number, or both (total flower number). Neither total nor staminate flower number is correlated with fruit mass; a significant relationship to fruit mass holds only for hermaphroditic flower production. Thus, the relationship between strong andromonoecy and large fruit is due to an underlying association of fruit size and hermaphroditic flower number. There is no consistent relationship between evolutionary changes in the strength of andromonoecy and changes in staminate or total flower production. This conclusion is supported by contrast correlations in which the strength of andromonoecy is expressed as a categorical variable. Evolutionary changes in the strength of andromonoecy are related to variation in hermaphroditic flower number but not to staminate or total flower number.

Ancestral reconstructions of flower numbers also are consistent with the interspecific and contrast correlation analyses. Evolutionary transitions to strong andromonoecy are associated with a decrease in the number of hermaphroditic flowers per inflorescence, whereas changes in staminate flower number are variable. For *S. pectinatum* (Fig. 3), for example, the evolution of strong andromonoecy involved only decreases in hermaphroditic flower number with staminate flower number remaining relatively unchanged. In contrast, for *S. quitoense* (Fig. 3), there was both a decrease in hermaphroditic and an increase in staminate flower number. Thus, while changes in staminate flower number are not consistently related to evolutionary changes in the strength of andromonoecy across the clade as a whole, there are particular instances where staminate flower production clearly plays a role in modulating the strength of andromonoecy. Evolutionary changes in staminate flower number can affect the strength of andromonoecy, and the evolution of this character should be studied from multiple perspectives, not just in relation to fruit size. Staminate flower production may be related to pollinator attraction (Janzen, 1977; Podolsky, 1993; Elle and Meagher, 2000; Connolly and Anderson, 2003), pollen donation (Primack and Lloyd, 1980; Harder and Thomson, 1989; Harder and Barrett, 1996; Elle and Meagher, 2000; Harder et al., 2000; Connolly and Anderson, 2003), and even herbivore avoidance (Bertin, 1982). Because the evolution of *S. quitoense* appears to have involved the addition of staminate flowers, this species would be a logical choice for further investigation of the fitness consequences of staminate flower production.

Production of staminate flowers, with their reduced ovary, is expected to result in recovery of resources that can be allocated to other, potentially fitness-enhancing functions (Primack and Lloyd, 1980; Bertin, 1982; Solomon, 1986; Spalik, 1991;

Emms, 1993; reviewed in Vallejo-Marín and Rausher, 2007). For species of *Lasiocarpa* and *Acanthophora,* the lack of association between staminate flower production and the strength of andromonoecy suggests that although strongly andromonoecious taxa make fewer hermaphroditic flowers (fewer flowers with fully developed ovaries), they do not consistently reallocate saved resources into increased staminate flower production. Similarly, Vallejo-Marín and Rausher (2007) found that resources recovered by not producing hermaphroditic flowers were not reallocated to increased staminate flower production, increased seed production, or to vegetative growth in andromonoecious *S. carolinense,* also a member of *Solanum* subgenus *Leptostemonum*.

Total flower production per inflorescence varies substantially among species of *Lasiocarpa* and *Acanthophora* (Table 2; Nee, 1979; Whalen et al., 1981). In their discussion of the diversification of andromonoecy, Whalen and Costich (1986) observed that, among New World taxa (primarily sections *Lasiocarpa* and *Acanthophora*), strongly andromonoecious species tended to produce fewer flowers per inflorescence than their more weakly andromonoecious relatives and suggested that increased strength of andromonoecy has been accompanied by a loss rather than a gain of flowers within inflorescences in this group. In contrast, the evolution of andromonoecy among *Solanum* in Australia may have involved the addition of staminate flowers and increases in total flower number (Anderson and Symon, 1989). We find no support for a regular association of either increases or decreases in total flower number with evolutionary changes in the strength of andromonoecy or with changes in fruit size. Although flower number per inflorescence appears to be an evolutionary labile character (it ranges from a mean of 2.6 in *S. pectinatum* to 16.5 in *S. stramoniifolium*), these differences are related to factors other than fruit size. Total flower number has been shown to affect pollinator attraction generally (Campbell, 1989; Ehrlen, 1991; Emms, 1993; Harder and Barrett, 1996) and female fitness in *S. carolinense* (Elle, 1999).

Correlation does not demonstrate causation, but the observed association between strong andromonoecy, large fruits, and fewer hermaphroditic flowers is consistent with the hypothesis that andromonoecy is a mechanism of pre-anthesis regulation of fruit set (Bertin, 1982; Whalen and Costich, 1986). As fruit become larger, fewer fruit can be matured, and fewer flowers with functional ovaries are produced. Fewer hermaphroditic flowers, in the absence of any consistent decreases in total flower number, results in stronger andromonoecy. Support for the fruit regulation hypothesis is all the more compelling because recent experimental studies have failed to find support for alternative hypotheses for the production of staminate flowers in *S. carolinense*. As noted, resources saved by the production of staminate (as opposed to hermaphroditic) flowers are not reallocated to fitness-enhancing functions. The same study also found that staminate flowers do not have increased pollen donation relative to hermaphroditic flowers (Vallejo-Marín and Rausher, 2007).

Evolution of a suite of correlated characters—Evolutionary changes in fruit mass, ovary size, and flower size are all positively correlated with one another in both interspecific and contrast analyses. That is, species with large flowers have large ovaries that develop into large fruit (Fig. 4). Genetic studies of tomato, *Solanum lycopersicum,* and its wild relatives provide insight into the correlation of ovary and fruit size. A single quantitative trait locus (QTL), *fw*2.2, has a major effect on fruit mass in tomato; allelic differences in *fw*2.2 increase fruit mass as much as 30% (Grandillo and Tanksley, 1996; Cong et al., 2002; Frary et al., 2002; Cong and Tanksley, 2006). Mature fruit size in tomato is determined by mitotic activity in both the pre-anthetic ovary and the developing fruit (Bohner and Bangerth, 1988; Gillaspy et al., 1993; Joubés et al., 1999; Cong et al., 2002; Bertin, 2004; Baldet et al., 2006), and *fw*2.2 is associated with modulation of mitotic activity at both of these stages (Frary et al., 2002). Thus, variation in *fw2.2* or a similar QTL will result in changes to both ovary and fruit size. The tomato locus *fw*2.2 is likely orthologous to the loci affecting fruit size in eggplant (*Solanum melongena*) and pepper (*Capsicum annuum*; Tanksley, 2004). Perhaps this locus, or a similar gene of large effect, may explain the differences in fruit size among *Solanum* species in sections *Lasiocarpa* and *Acanthophora* and underlie the correlated changes in fruit and ovary size.

Although the effect of *fw2.2* does not appear to extend to flower size, the joint evolution of flower and ovary size is not unexpected given that genetic correlations and developmental coregulation of floral organs is common (Elle, 1998; Armbruster et al., 1999; Ashman, 1999; Caruso, 2004; Anderson and Busch, 2006; reviewed in Ashman and Majetic, 2006). For example, analysis of andromonoecious *S. carolinense* revealed strong genetic correlations among corolla diameter, pistil length (ovary plus style and stigma), and anther length and width (Elle, 1998). Such genetic correlations are predicted to underlie the phenotypic correlations of floral organs observed among species of *Solanum* sections *Lasiocarpa* and *Acanthophora*.

Fruit, flower, and ovary size are not only correlated with one another, they are each correlated with the strength of andromonoecy. Although the observed relationship between fruit size and the strength of andromonoecy supports the conclusion that evolutionary changes in fruit size are generally accompanied by changes in the strength of andromonoecy, the cause of this relationship remains unknown. Because fruit size is related to ovary and flower size and also is likely related to other, unmeasured, variables (Harvey and Pagel, 1991; Price, 1997), any of these may be the targets of selection. For example, pollinators generally tend to prefer larger flowers (Bell, 1985; Conner and Rush, 1996; Galen and Newport, 1987; Stanton and Preston, 1988), and selection for increased flower size could, indirectly, result in changes in both fruit mass and the strength of andromonoecy.

Summary—Among the 13 species of *Solanum* studied here, fruit size is positively correlated with the strength of andromonoecy. This result persists after controlling for evolutionary history and is robust to uncertainty in phylogenetic relationships. In general, evolutionary changes in the strength of andromonoecy among members of sections *Acanthophora* and *Lasiocarpa* are associated with reductions in hermaphroditic flower production but not consistently with changes in staminate flower number. However, increases in staminate flower production have clearly led to strong andromonoecy in at least one species, *S. quitoense*. The association between large fruits, strong andromonoecy, and few hermaphroditic flowers is consistent with the hypothesis that andromonoecy provides a mechanism of pre-anthetic regulation of fruit set. The relationship of fruit mass to evolutionary changes in the strength of andromonoecy,

however, cannot be considered in isolation. Variation in fruit size is correlated with changes in both ovary and flower size, and each is correlated with the strength of andromonoecy. Any of these, or some other unmeasured variable, could be the target of selection underlying the diversification of andromonoecy. Indeed, discerning the causal relationships among such highly correlated traits remains a challenge to our understanding of reproductive evolution, especially in wild species.

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