Diversification of andromonoecy in *Solanum* section *Lasiocarpa* (Solanaceae): the roles of phenotypic plasticity and architecture[1]

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Quantitative analyses of sexual expression show extensive interspecific variation in the strength of andromonoecy (proportions of hermaphroditic and staminate flowers) among *Solanum* species in the monophyletic section *Lasiocarpa*. The roles of phenotypic plasticity and inter- and intra-inflorescence architecture in the diversification of andromonoecy within this small clade were analyzed. Four species that represent a range of expression of andromonoecy were examined. Staminate flowers produced within inflorescences ranged from 3% (*S. candidum*) to 7% (*S. ferox*) in weakly andromonoecious species and from 39% (*S. pseudolulo*) to 60% (*S. quitoense*) in more strongly andromonoecious species. Manipulation of fruit set on clonal replicates of multiple genotypes demonstrated variation among species for phenotypic plasticity. The strongly andromonoecious species, *S. pseudolulo* and *S. quitoense*, were not plastic and produced a large proportion of staminate flowers regardless of fruiting treatment, whereas *S. candidum* and *S. ferox* were phenotypically plastic and produced significantly more staminate flowers in the presence of developing fruit. Staminate flower production of all four species varied both within and among inflorescences. A greater proportion of staminate flowers were produced in distal (later produced) inflorescences. Within inflorescences, hermaphroditic flowers occurred in basal positions, whereas staminate flowers, when produced, occurred more distally. This pattern of staminate flower production is qualitatively the same in all species investigated; however, quantitative variation in the transition from hermaphroditic to staminate flower production within and among inflorescences is associated with variation in the strength of andromonoecy. At least three factors have contributed to the diversification of andromonoecy in section *Lasiocarpa* including the presence or absence of phenotypic plasticity in response to fruit set, quantitative variation in intra- and inter-inflorescence architectural effects, and total flower production.

Key words: andromonoecy; architecture; development; phenotypic plasticity; sexual systems; Solanaceae; *Solanum*.

Andromonoecy has historically been defined as a sexual system in which plants produce both hermaphroditic and female-sterile (hereafter, staminate) flowers. Andromonoecy occurs in approximately 4000 species of flowering plants from at least 33 families (21 listed in Yampolsky and Yampolsky, 1922; references for additional families available on request) and has clearly evolved independently in numerous plant lineages. Considerable attention has focused on the adaptive significance of andromonoecy (Bertin, 1982a; Whalen and Costich, 1986; Anderson and Symon, 1989; Spalik, 1991; Diggle, 1993, 1994; Emms, 1996; Emms et al., 1997). Andromonoecy is widely thought to provide a mechanism to independently adjust allocation to male and female function; individuals are assumed to vary production of hermaphroditic and staminate flowers in response to changes in resource availability (reviewed in Bertin, 1982a; but see Podolsky, 1993). Thus, andromonoecy is often considered a form of phenotypic plasticity. Regardless of the particular advantages of andromonoecy, however, the evolution of this sexual system requires the in-

novation of developmental mechanisms that allow for the production of two distinct floral types. Comparative developmental and morphological analyses of closely related species that vary in the magnitude of andromonoecy (i.e., in the relative production of hermaphroditic and staminate flowers) can identify those features that have been modified in association with the evolution and diversification of this sexual system. Once we understand *how* complex phenotypes such as andromonoecy evolve, we can create and test more refined hypotheses for *why* they evolve.

In the plant family Solanaceae, andromonoecy is well documented in *Solanum* subgenus *Leptostemonum* and has been reported for 13 of 22 described sections (Whalen and Costich, 1986). *Lasiocarpa* is a small section of 12 species, within subgenus *Leptostemonum*, that is strongly supported as monophyletic based on morphological, allozyme, karyotype, and chloroplast restriction site data (Heiser, 1972, 1987; Whalen and Caruso, 1983; Bernardello et al., 1994; Bruneau et al., 1995). Although all members of *Lasiocarpa* are andromonoecious, the numbers of hermaphroditic and staminate flowers produced among species in this section varies considerably (Whalen et al., 1981). Some species are characterized as weakly andromonoecious (e.g., *S. hirtum* Vahl., Diggle, 1993; *S. stramonifolium* Jacq., Whalen et al., 1981); that is, plants produce relatively few staminate flowers. In contrast, other species bear many staminate flowers and are described as strongly andromonoecious (e.g., *S. quitoense* Lam., Whalen and Costich, 1986; *S. vestissimum* Dunal., Whalen et al., 1981). The diversity of sexual expression among species in section *Lasiocarpa* makes this an ideal group for comparative analyses.

Detailed investigation of *Solanum hirtum* (section *Lasiocarpa*) has shown that sexual expression is phenotypically

plastic; fruit-bearing plants produce a greater proportion of staminate flowers than genetically identical plants that are prevented from producing fruit (Diggle, 1993). Because fruit development poses a significant drain on resources available for continued development (Lloyd, 1980), plasticity of sexual expression in *S. hirtum* is consistent with hypotheses for the evolution of andromonoecy that suggest that the production of staminate flowers is a mechanism for adjusting allocation to male and female function. As continued fruit production becomes resource-limited, subsequent production of staminate flowers allows reallocation of resources away from "costly" gynoecia toward increased male function, vegetative growth, or storage (reviewed in Bertin, 1982a; Whalen and Costich, 1986; Spalik, 1991). These analyses of *S. hirtum* indicate that consideration of plasticity should be integral in comparative studies of the expression of andromonoecy in section *Lasiocarpa*.

To compare andromonoecy and developmental plasticity among species, sexual expression must be characterized at multiple levels of morphological organization. In *S. hirtum* the occurrence of staminate flowers varied both within and among inflorescences. All inflorescences on fruit-bearing plants produced both hermaphroditic and staminate flowers; however, the proportion of staminate flowers increased in successively developing inflorescences (Diggle, 1994). We refer to this variation in sexual expression as an inter-inflorescence architectural effect. In addition, within inflorescences, flowers in basal positions were predictably hermaphroditic, that is, the phenotype of these flowers was fixed regardless of treatment. Only the phenotype of flowers in distal positions within inflorescences was plastic and varied with fruiting treatment. These flowers developed as hermaphroditic in the absence of fruit and as staminate on fruit-bearing plants (Diggle, 1994). We refer to variation in the developmental potential of individual flowers within inflorescences as an intra-inflorescence architectural effect (sensu Diggle, 1995). Both inter- and intra-inflorescence architectural effects varied among genotypes of *S. hirtum* and affected the magnitude of plasticity and the strength of andromonoecy. Therefore, we also ask how these architectural effects are expressed in other species in section *Lasiocarpa* and whether these effects contribute to the diverse expression of andromonoecy among species.

To investigate the potential roles of phenotypic plasticity and architectural effects in the diversification of andromonoecy, we studied sexual expression for four additional species in section *Lasiocarpa*: *Solanum candidum* Lindl., *S. ferox* var. *lasiocarpum* (Dunal) Miq., *S. pseudolulo* Heiser, and *S. quitoense* Lam. The four species were chosen to encompass wide variation in the degree of andromonoecy. Specifically, we consider four questions for each of these species. (1) What is the degree of andromonoecy and to what extent does andromonoecy vary among these closely related species? (2) Is sexual expression phenotypically plastic with respect to fruiting status (i.e., resource availability)? (3) How does inter-inflorescence variation affect whole plant sexual expression? (4) What is the distribution of hermaphroditic and staminate flowers within inflorescences, and is there a predictable architectural component of staminate flower production within inflorescences?

MATERIALS AND METHODS

Study species—*Solanum candidum*, *S. ferox* var. *lasiocarpum*, *S. pseudolulo*, and *S. quitoense* are shrubby, lignescent perennials included in section

Lasiocarpa of *Solanum* subgenus *Leptostemonum*. All members of section *Lasiocarpa* are sexually reproducing, self-compatible, and andromonoecious, producing both hermaphroditic and staminate flowers (Whalen et al., 1981). The four species included were chosen to incorporate variation within section *Lasiocarpa*. For example, vegetative size ranged from small, bushy species (*S. pseudolulo*, ~1.5 m tall, with considerable lateral branching) to larger, treelike species (*S. quitoense*, >3 m tall, with minimal lateral branching). Flower size and production also varied considerably. Flower production ranged from 5 or 6 flowers per inflorescence for *S. pseudolulo* and *S. ferox* (Whalen et al., 1981; J. S. Miller and P. K. Diggle, unpublished data) to >10 flowers per inflorescence for *S. candidum* and *S. quitoense*. Flowers from *S. quitoense* were also 60–80% larger compared to the other species.

Seed for *S. candidum* was obtained from L. Bohs (University of Utah, Salt Lake City, Utah, USA) and was collected from La Cangreja Reserve in Costa Rica (Bohs no. 98–104). *Solanum ferox* var. *lasiocarpum* was collected from Indonesia (M. Ansyar 9605), and seed was obtained from C. Heiser (University of Indiana, Bloomington, Indiana, USA). The Botanical Garden of Nijmegen, Netherlands, provided seed for *S. pseudolulo* (accession no. 824750021). Seed for *S. quitoense* was acquired in Quito, Ecuador by C. Heiser. Voucher specimens for all species are housed at the University of Colorado herbarium (COLO).

Experimental design—Plants were grown from seed and clonally replicated by vegetative cuttings to produce genetically identical plants. For *Solanum candidum*, *S. pseudolulo*, and *S. quitoense*, four replicate clones were produced from either six (*S. pseudolulo*) or eight (*S. candidum*, *S. quitoense*) genotypes for a total of 88 plants. For *S. ferox*, six genotypes were used, and eight replicate clones were produced per genotype (8 clones × 6 genotypes = 48 plants). All plants were grown in 11-L (3-gal) pots 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 Company, Marysville, Ohio, USA). Plants were watered daily with 150–200 ppm of Excel Magnitrate fertilizer (Scotts Company). Two (*S. candidum*, *S. pseudolulo*, *S. quitoense*) or four (*S. ferox*) replicates for each genotype were randomly assigned positions in each of two greenhouse rooms (110 and 111), and within each room these replicates were randomly assigned a fruiting treatment: +Fruit or −Fruit.

An important determinant of plant resource status is fruit set; plants with developing fruit have fewer resources available for growth and continued reproduction than plants with no developing fruit (Lloyd, 1980). Because inflorescences are produced continuously, fruits, flowers, and flower buds occur simultaneously on each branch, and experimental manipulation of plant fruiting status is an effective, biologically relevant way to manipulate resource status. For plants in the +Fruit treatment, all open hermaphroditic flowers were pollinated every other day using a mixture of pollen collected from several (≥3 genotypes) conspecific pollen donors. Hermaphroditic flowers remained open for 2–3 d; therefore, most flowers were pollinated at least twice, thus maximizing the potential for successful fertilization. In contrast, no flowers were pollinated on plants in the −Fruit treatment and any autogamously produced fruits were removed shortly after their initiation. Autogamous fruit production was rare in *S. ferox*, *S. pseudolulo*, and *S. quitoense*, but occurred occasionally in *S. candidum*.

Plants of these species have a predictable architecture; branches are sympodial and produce inflorescences sequentially and continuously. Two branches on each plant were haphazardly selected and censused every other day. Inflorescences were numbered from the base of the branch such that basal, early-developing inflorescences were numbered first. Floral positions within inflorescences were numbered distally from the basal-most position. Inflorescence position, flower position, floral sexual phenotype (i.e., hermaphroditic or staminate), and fruit production (+Fruit treatment only) were recorded for all flowers on 10 inflorescences on each of two marked branches per individual. Hermaphroditic flowers are easily distinguished from staminate flowers by their larger size and long-exserted styles that exceed the anthers (Whalen et al., 1981; Whalen and Costich, 1986; Diggle, 1991; J. S. Miller and P. K. Diggle, unpublished data). The experiment continued from July 2000 until
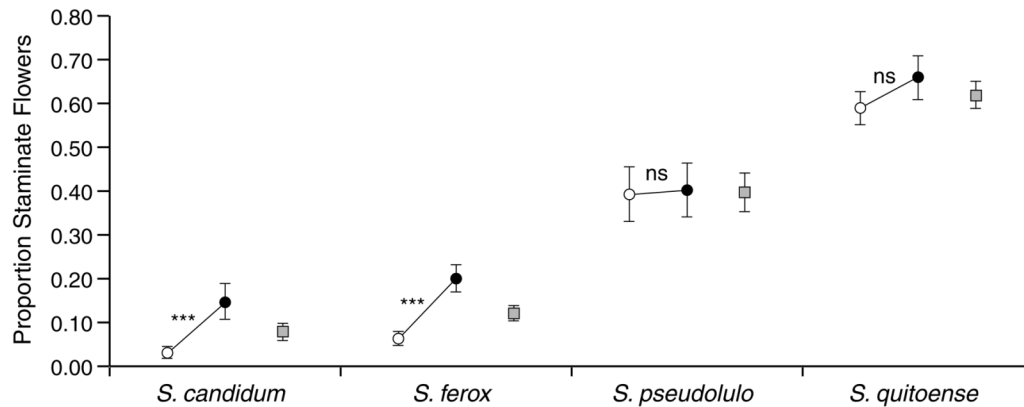
Fig. 1. The proportion of staminate flowers produced by four species in *Solanum* section *Lasiocarpa*. Plotted values are back-transformed means shown with 95% confidence intervals for genotypes in the −Fruit treatment (open circles), the +Fruit treatment (closed circles), and the grand means across both treatments (shaded squares). The main effect of fruiting treatment was significant for *S. candidum* ($F_{1,31} = 38.74$, $P = 0.0001$) and *S. ferox* ($F_{1,71} = 46.06$, $P = 0.0001$), but not for *S. pseudolulo* ($F_{1,9} = 0.24$, $P = 0.6343$) or *S. quitoense* ($F_{1,29} = 0.61$, $P = 0.4419$).

May 2001 for *S. candidum*, *S. pseudolulo*, and *S. quitoense* and from September 2001 to March 2002 for *S. ferox*.

Statistical analyses—To determine the effects of fruiting treatment and inter-inflorescence ontogeny on sexual expression, we first calculated the proportion of staminate flowers produced within each inflorescence for all inflorescences on marked branches. Proportions were arcsin-square-root transformed and analyzed as a repeated measures design using either PROC MIXED (*S. candidum*, *S. ferox*, and *S. quitoense*; Littell et al., 1996) or PROC GLM (*S. pseudolulo*; Littell et al., 1991) in SAS. Because inflorescence production occurred over time along branches, the repeated measure in these analyses was the proportion of staminate flowers produced within inflorescences, which were numbered from the earliest inflorescence (=1) to the last inflorescence (=10) along each branch. In the PROC MIXED analyses, effects included in the model were fruiting treatment (overall phenotypic plasticity), genotype, greenhouse room (overall block effect), inflorescence position (inter-inflorescence effect), and all interaction terms; the interactions of importance to our interpretation were genotype by treatment (genotypic variation for plasticity) and inflorescence by treatment (plasticity of inter-inflorescence variation). Because the PROC MIXED model was not appropriate for analysis of *S. pseudolulo* (i.e., the maximum likelihood model did not fit the observed data), we used PROC GLM to analyze data for this species. This model included fruiting treatment, genotype, greenhouse room, and all interactions as between-subject effects, as well as inflorescence position as the within-subjects effect. All of the interaction terms with inflorescence position were also included. Because PROC GLM excludes data from subjects with missing data, we included data from only the first eight inflorescences of *S. pseudolulo*.

For each species, we determined the effect of intra-inflorescence architectural variation on sexual expression by calculating the probability of producing a staminate flower at each floral position averaged over all inflorescence positions. Hermaphroditic flowers were assigned the number 0 and staminate flowers were assigned the number 1, and these values were averaged for each floral position within inflorescences. We used nonparametric Kendall rank correlations to determine if the probability of producing a staminate flower increased with increasing floral position within inflorescences.

RESULTS

Fruit production of pollinated plants—The percentage of hermaphroditic flowers that set fruit in the +Fruit treatment ranged from 23.4% ± 1.5% (means ± 1 SE, *N* = 807) for *Solanum pseudolulo* to 61.2% ± 1.2% (*N* = 1708) for *S. ferox*. *Solanum quitoense* and *S. candidum* matured 26.6% ± 2.0% (*N* = 489) and 31.7% ± 1.1% (*N* = 1848) of hermaph-

roditic flowers into fruit, respectively. No unpollinated plants of any species produced mature fruit.

Plasticity of sexual expression and variation among genotypes—Plasticity of sexual expression differed among species. *Solanum candidum* and *S. ferox* were phenotypically plastic; individuals of *S. candidum* and *S. ferox* with developing fruit produced significantly more staminate flowers than genetically identical individuals lacking fruit (Fig. 1). The fruiting treatment by greenhouse room interaction was significant for *S. candidum* ($F_{1,31} = 5.54$, $P = 0.025$). This interaction reflects the difference between fruiting treatments in the two greenhouse rooms: the +Fruit plants produced 6% more staminate flowers than −Fruit plants in room 110 and 19% more in room 111. Nevertheless, when greenhouse rooms were analyzed separately for *S. candidum*, staminate flower production was significantly higher for the +Fruit treatment compared to the −Fruit treatment in each room (room 110, $F_{1,15} = 17.01$, $P = 0.0009$; room 111, $F_{1,16} = 23.91$, $P = 0.0002$). In contrast to *S. candidum* and *S. ferox*, *S. pseudolulo* and *S. quitoense* were not plastic; staminate flower production did not depend on fruiting status (Fig. 1).

All genotypes of *S. candidum* and *S. ferox* in the +Fruit treatment produced more staminate flowers than genetically identical plants in the −Fruit treatment (Fig. 2A, B). For *S. candidum*, the magnitude of the response differed among genotypes (compare slopes in Fig. 2A); however, the difference was not significant (i.e., there was no treatment by genotype interaction; $F_{7,31} = 0.67$, $P = 0.70$). Hence, there was no genetic variation for plasticity. The treatment by genotype interaction for *S. ferox* was significant ($F_{5,71} = 3.28$, $P = 0.01$); however, this variation was contributed largely by a single, nonresponsive genotype (genotype 4; Fig. 2B).

In general, the nonplastic species showed more variation among genotypes in staminate flower production than the plastic species (Fig. 2C, D). There was significant variation among genotypes in the grand mean of the proportion of staminate flowers produced for the nonplastic species, *S. pseudolulo* ($F_{5,9} = 9.60$, $P = 0.002$) and *S. quitoense* ($F_{7,29} = 2.60$, $P = 0.03$), but not for the plastic species *S. candidum* ($F_{7,31} = 1.92$, $P = 0.10$) or *S. ferox* ($F_{5,71} = 0.89$, $P = 0.49$).
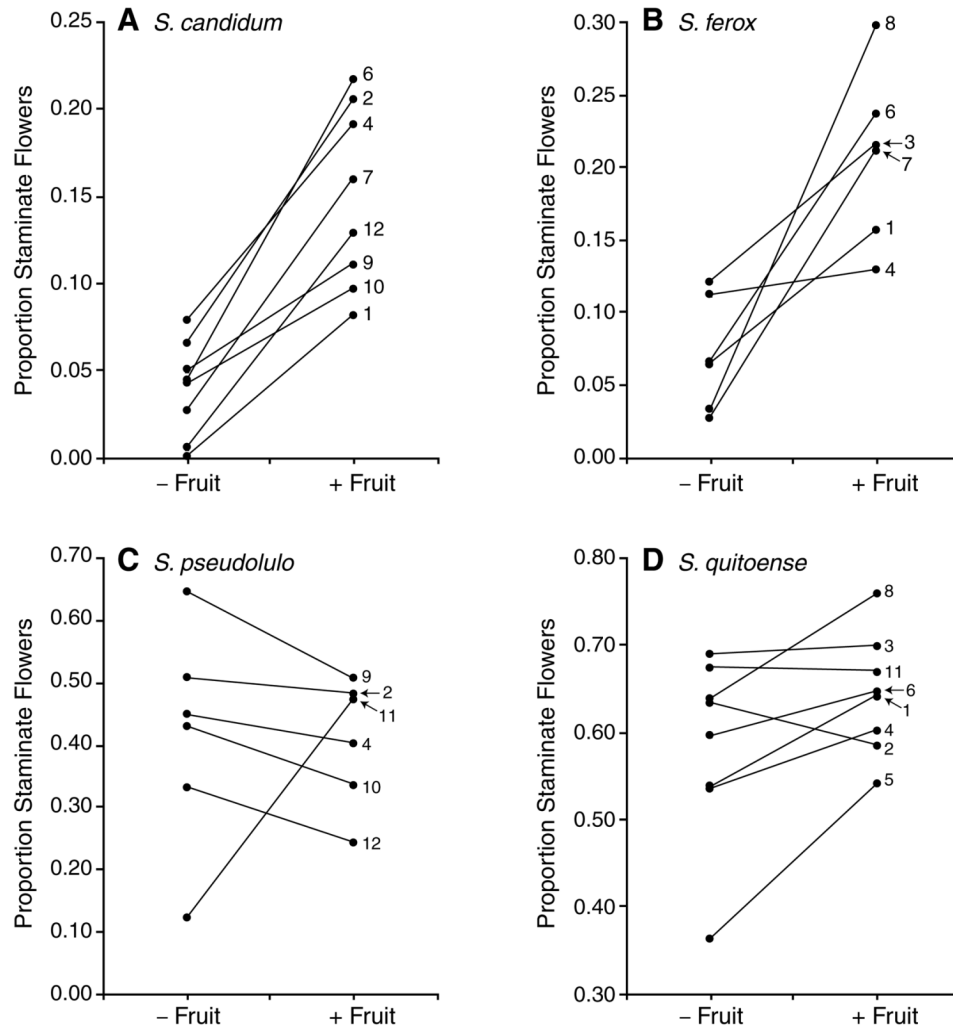
Fig. 2. Reaction norms for the proportion of staminate flowers produced within inflorescences for (A) *Solanum candidum*, (B) *S. ferox* var. *lasiocarpum*, (C) *S. pseudolulo*, and (D) *S. quitoense*. Plotted values are back-transformed means for each genotype in the two treatments. Numbers at right indicate the genotype identity. Note differences in the scale of the *y*-axes.

Inter-inflorescence effects—Inflorescence position had a strong and significant effect on staminate flower production for all four species. In *S. candidum* and *S. ferox*, the inflorescence effect depended on the fruiting treatment, and there was a significant inflorescence by treatment interaction for these species (*S. candidum*, $F_{9,197} = 8.10$, $P = 0.0001$; *S. ferox*, $F_{9,535} = 3.99$, $P = 0.0001$). Staminate flower production in the −Fruit treatment changed little (<15%) in successive inflorescences, whereas in the +Fruit treatment staminate flower production increased dramatically with inflorescence position (73% in *S. candidum* and 44% in *S. ferox*; Fig. 3A, B). For *S. pseudolulo* and *S. quitoense*, inflorescences in more distal positions produced significantly more staminate flowers (*S. pseudolulo*, $F_{7,63} = 10.84$, $P = 0.0001$; *S. quitoense*, $F_{9,158} = 6.69$, $P = 0.0001$; Fig. 3C, D); however, there were no significant interactions between inflorescence position and fruiting treatment for either species.

Intra-inflorescence effects—The probability of producing staminate flowers increased in distal floral positions within inflorescences for all four species. Specifically, staminate flower production was significantly positively correlated with floral position for *S. candidum* and *S. ferox* in both treatments (*S. candidum*, Tau > 0.84, $Z > 3.9$, $P < 0.0001$; *S. ferox*, Tau = 1.0, $Z > 3.7$, $P = 0.0002$), and this effect was more pronounced in the +Fruit treatment (Fig. 4A, B). There were similar architectural effects on the probability of producing staminate flowers for *S. pseudolulo* (Tau = 1.0, $Z = 3.46$, $P = 0.0005$; Fig. 4C) and *S. quitoense* (Tau = 0.509, $Z = 2.85$, $P = 0.0043$; Fig. 4D).

Block effect—There was a significant main effect of greenhouse room on sexual expression for three of the four species (*S. candidum*, $F_{1,31} = 27.26$, $P = 0.0001$; *S. ferox*, $F_{1,71} = 49.24$, $P = 0.0001$; *S. pseudolulo*, $F_{1,9} = 11.84$, $P = 0.007$). Genotypes of *S. candidum*, *S. ferox*, and *S. pseudolulo* grown in greenhouse room 111 produced, on average, 10% more staminate flowers compared to identical genotypes housed in greenhouse room 110. Though not statistically significant for *S. quitoense* ($F_{1,29} = 0.90$, $P = 0.3499$), genotypes in this species showed the same trend, producing 7% more staminate flowers in greenhouse room 111 compared to room 110.
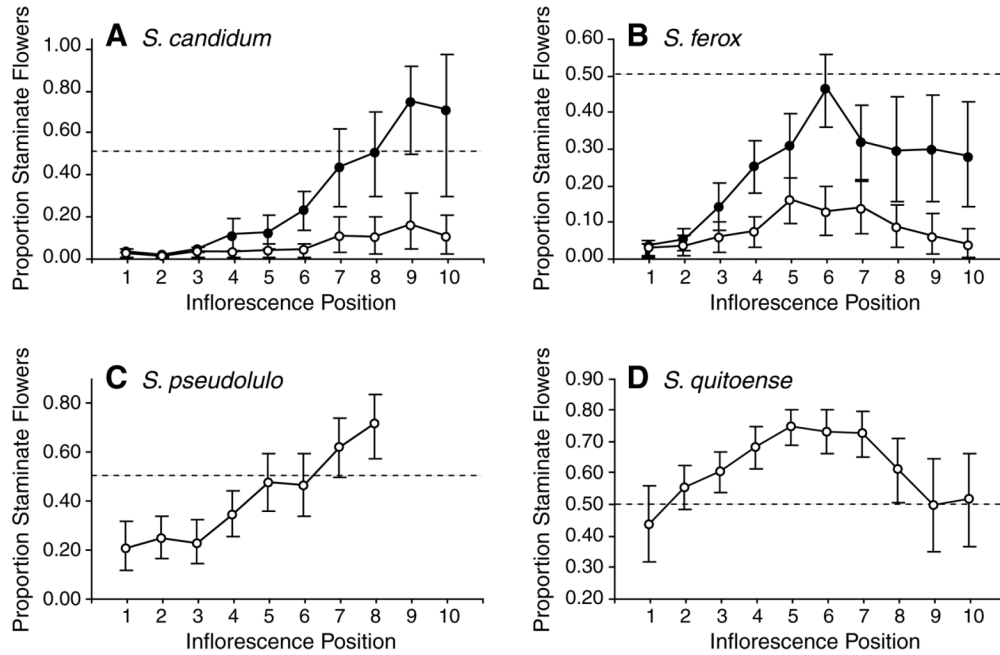
Fig. 3. Staminate flower production in successive inflorescence positions for (A) *Solanum candidum*, (B) *S. ferox* var. *lasiocarpum*, (C) *S. pseudolulo*, and (D) *S. quitoense*. For the plastic species, *S. candidum* and *S. ferox* var. *lasiocarpum*, open symbols represent the −Fruit treatment mean and closed symbols represent the +Fruit treatment mean. For the nonplastic species, *S. pseudolulo* and *S. quitoense*, the grand means are presented. Plotted values are back-transformed means shown with 95% confidence intervals. Note differences in the scale of the *y*-axes; dotted lines indicate 50% staminate flower production within inflorescences.
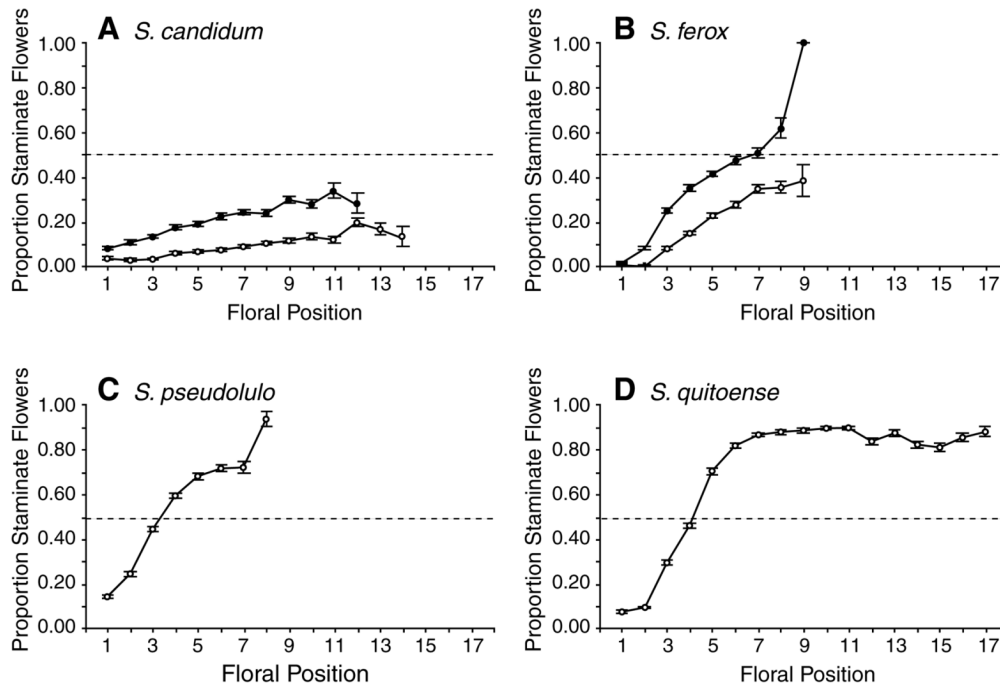
Fig. 4. Staminate flower production within inflorescences, averaged across all inflorescence positions, for (A) *Solanum candidum*, (B) *S. ferox* var. *lasio-carpum*, (C) *S. pseudolulo*, and (D) *S. quitoense*. For the plastic species, *S. candidum* and *S. ferox* var. *lasiocarpum*, open symbols represent the −Fruit treatment mean and closed symbols represent the +Fruit treatment mean. For the nonplastic species, *S. pseudolulo* and *S. quitoense*, the grand means are presented. Error bars are ±1 SE.

DISCUSSION

The 12 species of *Solanum* section *Lasiocarpa* are all andromonoecious and presumably inherited this sexual system from a common ancestor. Nevertheless, quantitative analyses of sexual expression for five species show extensive interspecific variation in the degree of andromonoecy. We argue below that evolutionary modification of developmental plasticity and inter- and intra-inflorescence architecture interact to produce the diverse expressions of andromonoecy observed among species of section *Lasiocarpa*.

Andromonoecy in Solanum section Lasiocarpa—The degree of andromonoecy differs widely among species in *Solanum* section *Lasiocarpa*. Choice of the appropriate metric for quantitative comparison among the species, however, is problematic. Although the −Fruit treatment may not be realistic in natural populations, we argue that comparisons among species should be made using the −Fruit treatment because patterns of sexual expression using data from plants without fruit measures their inherent tendency to produce staminate flowers. In addition, the −Fruit treatment is equivalent across species, whereas the +Fruit treatment may differ among species due to differential fruit production or fruit size. It should be noted, however, that the rank order of the strength of andromonoecy is the same regardless of the measure used for comparison (Fig. 1).

In the absence of fruit production, *S. candidum* and *S. ferox* (this study) and *S. hirtum* (Diggle, 1993) produce few staminate flowers (3%, 7%, and <1%, respectively; Fig. 1), and therefore should be considered weakly andromonoecious. In contrast, even in the absence of fruit production, *S. quitoense* is strongly andromonoecious and produces nearly 60% staminate flowers per inflorescence. *Solanum pseudolulo* is intermediate and produces 39% staminate flowers (Fig. 1). Although all of these species are typologically andromonoecious and are capable of producing both hermaphroditic and staminate flowers, they differ dramatically in the magnitude of expression of this sexual system, despite sharing a common origin of andromonoecy.

Plasticity in Solanum section Lasiocarpa—Plasticity of allocation to male and female function generally is thought to be an important component of the evolution of andromonoecy (reviewed in Bertin, 1982a) and is clearly the mechanism by which staminate flower production occurs in *S. hirtum* (Diggle, 1993). Yet, analyses of four additional species of *Lasiocarpa* reveal that staminate flower production is a phenotypically plastic response to fruit production in *S. candidum* and *S. ferox*, but is a fixed aspect of the phenotype in *S. quitoense* and *S. pseudolulo* (Fig. 1). Thus, andromonoecy and the production of staminate flowers in *Lasiocarpa* is not inevitably a plastic response to the presence of developing fruit.

The presence or absence of plasticity per se appears to be associated with differences in the strength of andromonoecy: plastic species are weakly andromonoecious, whereas staminate flower production is fixed in strongly andromonoecious species. Considering only the plastic species, we cannot determine whether variation in the magnitude of plasticity (the difference in staminate flower production between the two treatments) is associated with variation in the degree of andromonoecy; plasticity and the degree of andromonoecy are similar among *S. ferox*, *S. candidum*, and *S. hirtum*. Thus,

although plasticity is a mechanism for staminate flower production by some taxa within *Lasiocarpa*, differences in plasticity do not underlie the observed variation in andromonoecy.

Our results demonstrate that analyses of phenotypic plasticity are always context specific. Although the four species differed in their capacity to respond to the fruiting treatment, they all responded plastically to the different environmental conditions of the two greenhouse rooms. All species produced more staminate flowers in greenhouse room 111 compared to room 110, significantly so for *S. candidum*, *S. ferox*, and *S. pseudolulo*. The two rooms are physically adjacent to each other and both maintained a mean temperature of 21°C. However, room 111 was significantly more shaded than room 110 (159.0 ± 13.0 μmol vs. 264.3 ± 33.4 μmol, respectively; $F_{1,98}$ = 8.6, P = 0.004). Studies of other andromonoecious species have shown that decreased light is associated with staminate flower production (*Aesculus pavia*, Bertin, 1982b; *Solanum carolinense*, Solomon, 1985). In addition, population sex ratios in some diphasic orchids are female biased in open habitats and male biased in closed canopies (Gregg, 1975, 1978; Zimmerman, 1991). The intuitive (but untested) explanation is that plants growing under increased light have greater photosynthate availability and thus an enhanced ability to mature fruit. It would be advantageous for plants under such conditions to produce hermaphroditic flowers. Whatever the proximate cue, staminate flower production differed significantly among rooms and represents a distinct form of plasticity in sexual expression.

Architectural effects on sexual expression in section Lasiocarpa—All species of *Lasiocarpa* investigated bear staminate flowers in a predictable pattern that encompasses both within- and among-inflorescence variation. At the level of branches, a greater proportion of staminate flowers are borne in later-produced inflorescences. For *S. candidum* and *S. ferox*, much of this pattern is the result of plastic changes in sexual expression in response to fruiting treatment. Staminate flower production in basal inflorescences of plants in the −Fruit treatment was near zero and remained less than 15% even in the distal-most inflorescences. Among inflorescences of plants in the +Fruit treatment, however, staminate flower production increased by over 40% from basal to distal inflorescences (Fig. 3A, B). A similar pattern of inter-inflorescence variation in association with plasticity occurred in *S. hirtum* (Diggle, 1993). This pattern of increased staminate flower production in successive inflorescences is consistent with a plastic response by developing flowers to the presence of maturing fruit at earlier (more basal) inflorescence positions.

Staminate flower production in the nonplastic species, *S. pseudolulo* and *S. quitoense*, also increases in distal inflorescences (Fig. 3C, D); however, this pattern is not dependent on fruiting treatment, rather, it is a fixed aspect of the architecture of each branch. The pattern of inter-inflorescence increase in the proportion of staminate flowers in the nonplastic species is qualitatively similar to that of fruit-bearing plants of the plastic species (*S. candidum* and *S. ferox*; Fig. 3), though staminate flower production commences at earlier (more basal) inflorescences in the nonplastic species. For example, the first inflorescence bears 20% (*S. pseudolulo*) to 40% (*S. quitoense*) staminate flowers in nonplastic species compared to near zero in the plastic species (compare Fig. 3A, B to C, D). Strong andromonoecy exhibited by *S. pseudolulo* and *S. quitoense* is

due, in part, to the onset of staminate flower production at early inflorescence positions.

Within inflorescences of each of the four species, staminate flowers can be produced at all floral positions; however, the probability is very low at basal positions and increases distally (Fig. 4). Thus, the general pattern is one of hermaphroditic flowers in basal positions, and staminate flowers, if produced, in terminal portions of each inflorescence. Although the pattern is qualitatively similar, there are quantitative differences in the average intra-inflorescence pattern of staminate flower production among the four species and between treatments of the plastic species. Two indices can be used for comparison: the flower position at which the probability of producing a staminate flower exceeds 50% (dotted line in Fig. 4) and the probability of staminate flower production in the distal-most positions. In inflorescences of the strongly andromonoecious species, *S. quitoense* and *S. pseudolulo*, staminate flower production occurs early (>50% probability by flower position 4–5) and, in the distal-most positions, the probability of staminate flowers exceeds 80% (Fig. 4C, D). In contrast, in weakly andromonoecious *S. ferox*, staminate flower production does not exceed 50% until flower position 7 in fruit-bearing plants and never exceeds 50% in nonfruiting plants (Fig. 4B). In *S. candidum*, despite a distal increase in staminate flower production, the average probability never exceeds 50% at any position in either treatment (Fig. 4A). Thus, within inflorescences, strong andromonoecy is associated with an earlier transition from hermaphroditic to staminate flower production and a greater probability of staminate flowers in distal-most positions.

The preceding analysis considers the intra-inflorescence pattern averaged across all 10 inflorescences per branch (Fig. 4). While this summary allows for explicit quantitative comparisons, it obscures the significant variation in staminate flower production among inflorescences. Figure 5 depicts the combined effects of both sources of variation in sexual expression: intra- and inter-inflorescence architectural effects. This representation confirms that staminate flowers are produced distally within inflorescences and that the transition from hermaphroditic to staminate flower development occurs at more basal floral positions within later, more distal inflorescences. Moreover, Fig. 5 emphasizes that strong andromonoecy is the result of an earlier transition from hermaphroditic to staminate flower production both within and among inflorescences. For example, the strongly andromonoecious *S. quitoense* bears staminate flowers on the first inflorescence, and within that inflorescence, the transition to staminate flowers occurs at flower position six (Fig. 5D). In contrast, the weakly andromonoecious species produce staminate flowers at later inflorescences (2 or 5) and later flower positions (8 or 11; *S. ferox* and *S. candidum*, respectively; Fig. 5A, B). These comparisons indicate that diversification of andromonoecy has occurred by quantitative variation in both inter- and intra-inflorescence positional effects on floral development.

The number of flowers borne on each inflorescence also can contribute to differences in the strength of andromonoecy. Hermaphroditic flower number is comparable for *S. pseudolulo* and *S. quitoense* (Fig. 5C, D); however, the more strongly andromonoecious *S. quitoense* produces considerably more (typically staminate) flowers per inflorescence. Based on an informal survey of the genus *Solanum*, Whalen and Costich (1986) predicted that strong andromonoecy would not be associated with the production of excess staminate flowers.
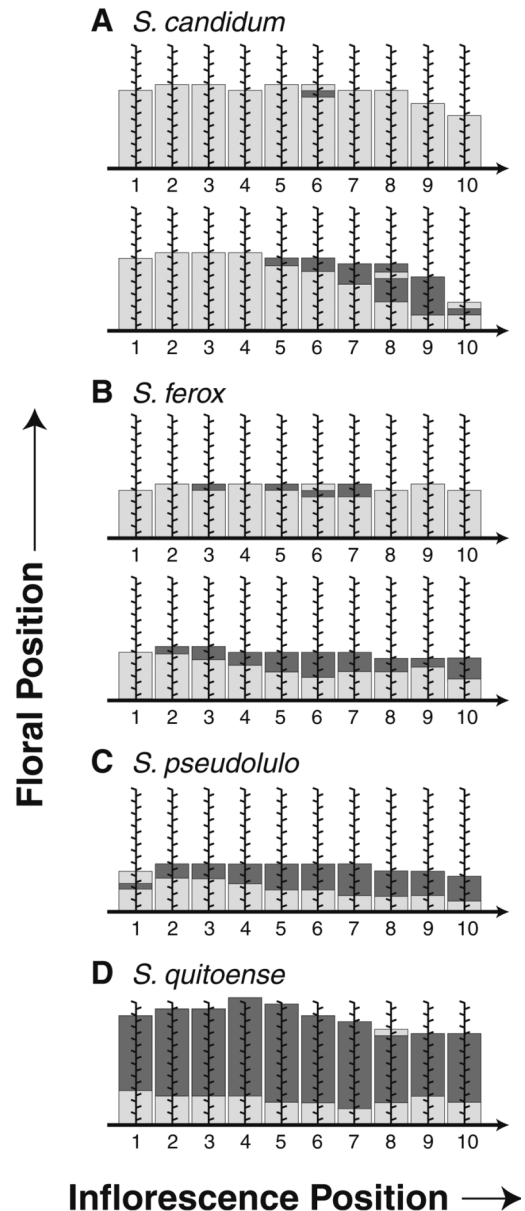

Fig. 5. Intra- and inter-inflorescence effects on staminate flower production for (A) *Solanum candidum*, (B) *S. ferox* var. *lasiocarpum*, (C) *S. pseudolulo*, and (D) *S. quitoense*. Inflorescence position along the branch is shown schematically along the horizontal axis (for the first 10 inflorescences). Floral position within inflorescences increases vertically. Light shading indicates a <50% probability of producing a staminate flower, whereas dark shading indicates a ≥50% probability of producing a staminate flower. For the plastic species, *S. candidum* and *S. ferox* var. *lasiocarpum*, the top panel is the −Fruit treatment and the lower panel is the +Fruit treatment. For the nonplastic species, *S. pseudolulo* and *S. quitoense*, the grand means are presented.

Comparisons among more closely related species shows this to be incorrect. Clearly, the addition of flowers, which are predominantly staminate, increases the degree of andromonoecy for *S. quitoense* (Fig. 5D).

Implications for andromonoecy in Solanum—Quantitative variation within an otherwise uniform architectural pattern appears to underlie differences in sexual expression within *Solanum* section *Lasiocarpa*. This model may be extended to

other members of the genus. General branching architecture (sensu Hallé et al., 1978) is quite uniform throughout the genus *Solanum*: branches grow sympodially with each sympodial unit bearing a characteristic number of leaves and terminating in an inflorescence (Child, 1979; Child and Lester, 1991). Thus, each leafy branch produces an indeterminate succession of inflorescences and typically bears fruits, flowers, and floral primordia simultaneously. Within the genus, andromonoecy has evolved and diversified within the context of this stereotypical morphology. In all described andromonoecious *Solanum* (belonging to different sections or even to different subgenera and likely representing more than one origin of andromonoecy), staminate flowers occur predominantly in distal positions within inflorescences (*S. torvum*, Hossain, 1973; *S. sodomeum* and *S. campanulatum*, Symon, 1979; *S. marginatum*, Dulberger et al., 1981; section *Lasiocarpa*, Whalen et al., 1981; *S. paliacanthum*, Coleman and Coleman, 1982; *S. carolinense*, Solomon, 1985; references to additional species in Whalen and Costich, 1986 and Anderson and Symon, 1989). Other patterns of staminate flower production, for example, basal staminate and distal hermaphroditic flowers within inflorescences or the production of exclusively hermaphroditic and exclusively staminate inflorescences within the same branch, have never been described for *Solanum*. Based on these observations, it is likely that what variation in sexual expression exists among andromonoecious species of the genus as a whole depends on the types of quantitative variation in architectural effects described here for section *Lasiocarpa*.

Architectural effects may also have played a critical role in the evolutionary transition from hermaphroditism to andromonoecy in *Solanum*. In many hermaphroditic species (regardless of taxon), fruit set is reduced or absent at distal positions within inflorescences (reviewed in Diggle, 1995, 2002); thus, many hermaphroditic taxa are functionally andromonoecious. Intra-inflorescence variation in female function has not been investigated explicitly in hermaphroditic species of *Solanum*; however, fruit size declines dramatically within inflorescences of cultivated tomato (Bertin, 1995), and distal hermaphroditic flowers in species of section *Lasiocarpa* rarely set fruit (P. K. Diggle, personal observation). Within *Solanum*, intra-inflorescence declines in female function may be an evolutionary antecedent of andromonoecy. If so, then the transition from functional to morphological andromonoecy would require only the origin of a developmental mechanism for preanthesis termination of ovary development in flowers that are already functionally female-sterile.

Evolutionary dynamics of plasticity—Although variation in the magnitude of plasticity may not underlie species-level variation in andromonoecy, we found variation in plasticity per se. Within the small section *Lasiocarpa*, staminate flower production is a phenotypically plastic response to fruit production in some species and a fixed aspect of the phenotype in others. Interestingly, the architectural pattern of staminate flower production is qualitatively similar in nonplastic species and fruit-bearing plants of the plastic species. There is a transition from hermaphroditic to staminate flower production within each inflorescence, and this transition occurs earlier (at more basal positions) on successive inflorescences. Thus, it is qualitatively the same phenotype that is fixed in some species and produced as a plastic response to fruit set in others. The pressing issue for future research is to understand the sequence of evolutionary transitions between these phenotypes. Because andromon-

oecy is typically assumed to be a form of plasticity, traditional hypotheses would predict that andromonoecy arose in the ancestor of *Lasiocarpa* as a plastic response and has become a fixed developmental pattern in some species.

We also found an association between weak andromonoecy and plasticity and between strong andromonoecy and fixed phenotypes. The association between plasticity and the degree of andromonoecy may be related to developmental constraints imposed by the architecture of *Solanum*. Given that inflorescences invariably contain both hermaphroditic and staminate flowers, an effective way to increase staminate flower production is to produce staminate flowers at earlier (more basal) positions both within and among inflorescences. Moreover, for the plastic species, if initiation of fruit development is the proximate cue for staminate flower development, then the production of staminate flowers will not be possible until later in branch ontogeny after significant numbers of fruit producing hermaphroditic flowers have developed. Hence, plastic plants may necessarily produce more hermaphroditic flowers relative to staminate flowers and will be classified as weakly andromonoecious.

Conclusions—That flowering plants as a group possess an enormous diversity of sexual systems is well known (Darwin, 1877). Surprisingly, the expression of a single sexual system can vary widely, even among members of a small clade. Andromonoecy has been defined typologically as a single phenotype, that is, the presence of both hermaphroditic and staminate flowers on individual plants. Analysis of *Solanum* section *Lasiocarpa* shows that andromonoecy clearly varies among species. The common ancestor of these species was likely andromonoecious, thus the variation documented here represents evolutionary diversification from a single "andromonoecious phenotype." At least three factors contribute to the diversification of sexual expression in this group, including the presence or absence of phenotypic plasticity in response to fruit set, intra- and inter-inflorescence architectural effects, and total flower production. Consideration of the stereotypical branching architecture of the genus *Solanum* and the recurring intra- and inter-inflorescence pattern of staminate flower production among all andromonoecious species indicates that these factors may also have been important in the evolutionary dynamics of andromonoecy in the genus as a whole.

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