

Architectural effects on floral form and function: a review

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The modular or metameric nature of plant growth has had profound consequences for the ways in which morphology has been studied and characterized. Because plants appear to be constructed of repeated units, we tend to think of these units as inherently similar. In this review, I argue that the default assumption, that plant metamers are similar, is in error, and that understanding the sources of variation among metamers is critical to understanding plant morphology and morphological diversification. A literature survey identified studies of 65 species in 27 families that demonstrated that features of the corolla, androecium, and/or gynoecium show significant intra-inflorescence variation that is attributable to flower position alone. A pattern of proximal to distal decline in size or mass is most common, however increases also occur. Moreover, the different organ whorls within a flower can vary independently of one another, leading to dramatic changes in floral function within inflorescences. Such positional variation may be the “raw material” for more pronounced intra-inflorescence diversification, such as that observed in monoecious taxa, or in syn-organized inflorescences.

The modular or metameric nature of plant growth has had profound consequences for the ways in which morphology has been studied and characterized. Because plants appear to be constructed of repeated units, we tend to think of these units as inherently similar. Developmentally, however, plant metamers are initiated sequentially; they are each produced in a distinct positional and historical (ontogenetic) milieu, and both of these factors potentially can influence the phenotype and function of metamers (Diggle, 1994; Watson & al., 1995). This phenomenon, in which the fate of a developing primordium depends upon where and when it is produced and what events have preceded it during the ontogeny of the organism, can be termed “ontogenetic contingency” (Diggle, 1994; Watson & al., 1995). The contingent nature of plant phenotypes is clearly a concern to those who wish to characterize morphology for systematic analysis or any other purpose. Below, I review the literature on intra-individual variation in reproductive characters and show that position alone can account for a significant amount of morphological and functional variation among flowers and fruits.

Biologists have long recognized that flowers and fruits produced by individual plants can vary. For example, fruit maturation almost universally declines from basal (earliest produced) to distal (latest produced) flower positions within an inflorescence. Likewise, fruit size, seeds per fruit, flower size, ovary size, ovule number, stamen number, and pollen production all have been observed to decline in a proximal to distal pattern (reviewed in Herrera, 1991; Ashman, 1992; Wolfe, 1992; Brunet & Charlesworth, 1995; Diggle, 1995, 1997; Guitián & Navarro, 1996). This variation has largely been assumed to be the result of phenotypically plastic responses to the presence of developing fruit. Within an inflorescence, basal flowers often initiate fruit before distal ones reach anthesis. Due to this temporal precedence, basal fruits become strong sinks for the resources necessary for maturation, and nutrient supply to distal flowers and fruits is reduced. In addition, distal flowers and fruits are located further from the source of nutrients. Both temporal and spatial effects on resource supply may adversely affect development. The result may be smaller flowers and fruits, or abortion of these structures (e.g., Lloyd, 1980; Stephenson, 1981).

Implicit in this interpretation is the assumption that all flowers within an inflorescence have equal developmental and reproductive potentials. That is, in the absence of resource preemption by basal fruits there is no variation in form and function among hermaphrodite flowers within inflorescences, and all intra-inflorescence variation is phenotypic plasticity. An alternative explanation should be tested before this plasticity hypothesis is accepted: proximal to distal variation in floral form and/or reproductive potential is due to positional variation inherent in the architecture of plant axes. This type of variation has been termed an “architectural effect” (Diggle, 1995, 1997).

In order to assess the contributions of architecture and plasticity to intra-inflorescence variation, proximal to distal variation in both fruiting and non-fruiting plants must be measured. What is the pattern of variation in the absence of resource pre-emption by developing fruits? A simple experimental design consists of two treatments: one in which all flowers are pollinated and allowed to set fruit and a second in which flowers are prevented from producing fruit. The differences in morphology or function among flowers of fruit-bearing plants is a measure of total variation (variation that is typically attributed to

plastic responses to resource competition). Morphological or functional variation measured among flowers of non-fruiting plants occurs in the absence of developing fruit, and so is attributable to architecture. Finally, in order to assess true plasticity, flowers at equivalent positions within inflorescences of the contrasting treatments are compared. In this comparison, positional variation is controlled and differences in morphology or function are due to the effects of treatment, in this case, the presence of developing fruit (see diagrams in Diggle, 1997).

A thorough search of the literature in the mid-1990s (Diggle, 1995, 1997) revealed that few studies of intra-inflorescence variation controlled for architectural effects in their analyses. The few studies that did, however, demonstrated that architectural effects do occur and suggested that they may be prevalent among flowering plants (Macnair & Cumbes, 1989; Thomson, 1989; Diggle, 1991; Ashman, 1992; Wolfe, 1992; Mossop & al., 1994; Brunet & Charlesworth, 1995). These studies indicated that architectural effects can mimic plasticity, and that in the absence of an architectural analysis, the importance of resource competition as a source of variation in reproductive characters is dramatically over-estimated. Moreover, architectural effects can also mask plasticity or cause misinterpretation of the direction of plastic responses (Diggle, 1997). Thus, if we are to understand the sources of variation in floral form and function, it is imperative to consider the extent and occurrence of architectural variation.

In the intervening years the number of studies that explicitly incorporate architectural analyses has increased substantially. For this symposium, I have scored the literature on plant reproduction for such studies and report information on architectural variation in a total of 65 species in 27 families. This analysis is not intended to suggest that phenotypically plastic reallocation of resources within inflorescences of fruit-bearing plants does not occur, clearly it does, and the effects are profound (reviewed in Stephenson, 1981; Lee, 1988; Diggle, 1995). Rather, my goal is to show that resource competition is only one of many factors that influence the development, morphology, and function of flowers and that variation due to position alone is a significant and prevalent feature of reproductive phenotypes.

Materials and methods

This review includes all studies of intra-inflorescence variation in flower structure or function that incorporate an explicit control for architectural effects, regardless of the outcome (i.e., those that found positional variation and those that did not). Additional studies are also included that either contain other sorts of evidence that resource competition is not the sole source of observed variation or that document patterns of variation inconsistent with intra-inflorescence resource competition (such as proximal to distal increases in flower or fruit size or fruit production). Not included are reports of proximal to distal declines based on observations of only fruit-bearing plants.

The individual studies examined different sets of reproductive characters in different ways (the analysis of architectural effects was generally not the primary goal of the study). In order to summarize these very diverse datasets, the reproductive characters were cate-

gorized and tabulated as follows. “Corolla” includes any measurement of corolla or petal length, width, or mass; “Gynoecium” includes size or mass of the ovary or gynoecium as a whole; “Ovule” is ovule number; “Androecium” includes stamen number, size, or mass; “Pollen” includes pollen number or mass; “Fruit” includes fruit length, mass, seed number per fruit, or total seed mass; “Maturation” includes fruit or seed maturation. The entries in the columns of the table indicate the pattern of intra-inflorescence variation observed in the absence of fruit set, i.e., in the absence of resource competition: “D” indicates a pattern of proximal to distal decline in that character, “I” indicates an increase, “C” shows that that character was constant or invariant with position in that study; and “V” indicates that there was variation but that it was not directional (erratic with respect to position). Characters not assessed in a study are denoted by a dot.

Results

Results of this literature survey are summarized in Table 1. Variation in fruit maturation is the most commonly studied feature of inflorescences (there are more entries for ovule number, but a large proportion of these come from the single preliminary study of Thomson, 1989). Thirteen studies demonstrated conclusively that observed patterns of proximal to distal decline in fruit or seed production were not attributable to resource competition alone, rather, flowers varied in their inherent capacity to form a mature fruit. Surprisingly, an additional eight studies detected a pattern of greater fruit production in distal flowers. In three species with proximal to distal increases in fruit maturation, *Narcissus dubius* (Worely & al., 2000), *Ipomopsis aggregata* (Brody & Morita, 2000), and *Euphorbia characias* (Espadaler & Gómez, 2001), distal flowers reach anthesis earlier than basal flowers. These studies did not include non-fruiting controls so they are unable to distinguish between resource pre-emption due to the temporal precedence of distal flowers and architecture per se as sources of variation in fruiting. In four of the remaining five species with distal increases in fruit maturation, *Yucca filamentosa* (Huth & Pellmyr, 1997), *Y. mckelveyana* (Sutherland, 1987), *Impatiens capensis* (Waller, 1982), and *Phytolacca rivinoides* (Byrne & Mazer, 1990), the increase occurs despite a pattern of proximal to distal anthesis. In these taxa, the direction of variation (proximal to distal increase) is inconsistent with an hypothesis of resource competition between early basal and later distal flowers. If these four species are added to the thirteen found experimentally to have proximal to distal declines in fruit developmental potential, then there is a total of 17 studies that have demonstrated architectural effects on fruit maturation. In contrast, 13 studies demonstrated experimentally that all flowers have equal capacity to set fruit in the absence of resource competition and that, in these species, observed patterns of variation in fruit or seed maturation can, indeed, be attributed solely to resource competition among flowers and fruits.

In addition to architectural variation in the ability of a flower to produce a mature fruit, fruit characteristics also differ with position. Thirteen studies examined variation in fruit size (mass or length) or seed number and all but one (*Euphorbia characias*; Espadaler & Gómez, 2001) found that these declined within inflorescences even in the

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Table 1. Patterns of intra-inflorescence variation attributable to position alone. Column heading abbreviations are: C = Corolla, G = Gynoecium, O = ovule number, A = Androecium, P = pollen, F = fruit length or mass, M = fruit maturation. Entries in the columns indicate direction of proximal to distal variation: I = increase, D = decline, C = constant, V = variable (non-directional). The dot (•) indicates that the trait was not examined. Superscripts refer to anything unusual about the dataset or taxon. In particular, some datasets that did not use an architectural control are included because the pattern of variation is inconsistent with resource competition. Also noted are entries from a preliminary dataset with very low sample sizes, and variation in other characters not included as headings in the table.

Taxon	C	G	O	A	P	F	M	Reference
Agavaceae								
<i>Yucca filamentosa</i> ¹	•	•	•	•	•	•	I	Huth & Pellmyr, 1997
<i>Y. mckelveyana</i> ¹	•	•	•	•	•	•	I	Sutherland, 1987
Amaryllidaceae								
<i>Narcissus dubius</i> ^{1,2}	I	•	I	•	•	•	I	Worley & al., 2000
Apiaceae								
<i>Pancreatium maritimum</i>	•	•	•	•	•	•	C	Medrano & al., 2000
Balsaminaceae								
<i>Impatiens capensis</i> ¹	•	•	•	•	•	•	I	Waller, 1982
Bignoniaceae								
<i>Catalpa speciosa</i>	•	•	•	•	•	•	C	Stephenson, 1979, 1980
Boraginaceae								
<i>Cryptantha flava</i>	•	•	•	•	•	•	D	Casper, 1984
Brassicaceae								
<i>Alliaria petiolata</i>	•	•	•	•	•	•	C	Susko & Lovett-Doust, 1999
<i>Arabidopsis thaliana</i>	I	C	•	I	•	•	•	Diggle, 1997
<i>Raphanus sativus</i> ³	•	•	D	•	D	•	•	Young & Stanton, 1990
Campanulaceae								
<i>Campanula rapunculoides</i> ⁴	C	•	D	•	C	•	•	Vogler & al., 1999
Caprifoliaceae								
<i>Diervilla lonicera</i>	•	•	I	•	•	•	•	Thomson, 1985
Caryophyllaceae								
<i>Petrocoptis grandiflora</i>	•	•	D	•	•	•	C	Guitian & Navarro, 1995
Euphorbiaceae								
<i>Euphorbia characias</i> ²	•	•	•	•	•	I	I	Espadaler & Gómez, 2001
Fabaceae								
<i>Ceratonia siliqua</i>	•	•	•	•	•	•	C	Arista & al., 1999
<i>Glycine max</i>	•	•	•	•	•	•	D	Huff & Dybing, 1980
<i>Lupinus luteus</i>	•	•	D	•	•	D	•	Van Stevenick, 1957
Fumariaceae								
<i>Corydalis ambigua</i> ⁵	D	D	D	C	•	•	C	Kudo & al., 2001
Hydrophyllaceae								
<i>Hydrophyllum appendicula</i>	D	•	•	•	•	D	•	Wolfe, 1992

Table 1 (continued).

Taxon	C	G	O	A	P	F	M	Reference
Lamiaceae								
<i>Lavandula stoechas</i>	D	D	C	Herrera, 1991
Liliaceae								
<i>Alstroemeria aruia</i>	.	.	D	.	.	.	D	Ladio & Aizen, 1999
<i>Blanfordia grandiflora</i>	.	.	D	.	.	.	C	Ramsey, 1997
<i>Brodiaea douglasii</i> ^{4, 6, 7}	.	.	D	Thomson, 1989
<i>Buchardia umbellata</i> ⁸	.	.	D	Thomson, 1989
<i>Bulbine bulbosa</i> ^{4, 7, 8}	.	.	D	Thomson, 1989
<i>Calochortus gunnisonii</i> ²	.	.	D	Thomson, 1989
<i>C. leichtlinii</i> ⁹	.	.	D	.	.	.	C	Holtsford, 1985
<i>C. leichtlinii</i> ¹⁰	.	.	D	.	.	.	D	Holtsford, 1985
<i>Chamaescilla corymbosa</i> ¹¹	.	.	D	Thomson, 1989
<i>Clintonia borealis</i>	.	.	D	.	.	.	D	Thomson, 1989
<i>Convallaria majalis</i> ¹¹	.	.	D	Thomson, 1989
<i>Erythronium grandiflorum</i>	.	.	D	.	D	.	C	Thomson, 1989
<i>Fritillaria pudica</i> ⁸	.	.	D	Thomson, 1989
<i>Gagea lutea</i>	D	Nishikawa, 1997
<i>Hyacinthoides non-scripta</i>	D	Corbet, 1998
<i>Maianthemum canadense</i>	.	.	C	Thomson, 1989
<i>Medeola virginiana</i>	.	.	D	Thomson, 1989
<i>Narthecium asiaticum</i> ¹²	D	D	D	D	C	.	D	Ishii & Sakai, 2001, 2002
<i>Polygonatum odoratum</i>	.	.	D	.	.	D	C	Gutián & al., 2002
<i>P. pubescens</i> ¹¹	.	.	D	Thomson, 1989
<i>Uvularia grandiflora</i> ^{2, 11}	.	.	D	Thomson, 1989
<i>Wurmbeckia dioica</i> ^{4, 7}	.	.	D	Thomson, 1989
<i>Zigadenus paniculatus</i> ¹³	.	.	V	Emms, 1993
Malvaceae								
<i>Sidalcea oregana</i>	D	.	D	D	.	.	.	Ashman, 1992
Onagraceae								
<i>Clarkia unguiculata</i> ¹⁴	C	.	D	.	.	C	C	Mazer & Dawson, 2001
<i>Epilobium angustifolium</i> ¹⁵	Sargent & Roitberg, 2000
<i>E. dodonaei</i>	.	.	D	Stocklin & Favre, 1994
<i>E. fleischeri</i>	.	.	D	Stocklin & Favre, 1994
<i>E. montanum</i>	.	.	D	Harper & Wallace, 1987
Orchidaceae								
<i>Aspasia principissa</i>	D	C	Zimmerman & Aide, 1989
<i>Dactylorhiza maculata</i>	D	.	.	.	D	D	.	Vallius, 2000
<i>Myrosmodes cochleare</i>	D	Berry & Calvo, 1991
Phytolaccaceae								
<i>Phytolacca americana</i>	D	.	McDonnell & al., 1984
<i>P. rivinoides</i>	I	Byrne & Mazer, 1990
Poaceae								
<i>Hordeum vulgare</i>	.	D	.	.	.	D	D	Cottrell & Dale, 1984

Table 1 (continued).

Taxon	C	G	O	A	P	F	M	Reference
Polemoniaceae								
<i>Ipomopsis aggregata</i>	•	•	•	•	•	•	I	Brody & Morita, 2000
Proteaceae								
<i>Banksia spinulosa</i> ¹	•	•	•	•	•	D	D	Vaughton & Ramsey, 1997; Vaughton, 1993
<i>Telopea speciosissima</i>	•	•	•	•	•	•	C	Goldingay & Whelan, 1993
Ranunculaceae								
<i>Aquilegia caerulea</i>	D	•	•	C	D	•	D	Brunet, 1990; Brunet & Eckert, 1998
Rosaceae								
<i>Fragaria virginiana</i> ⁴	D	•	D	•	D	•	•	Ashman & Hitchens, 2000
<i>Pyrus malus</i>	•	•	•	•	•	•	I	Heinicke, 1917
Scrophulariaceae								
<i>Linaria canadensis</i>	•	•	•	•	•	D	•	Wolfe & Denton, 2001
<i>Mimulus guttatus</i> ⁴	D	D	•	•	D	D	•	Macnair & Cumbes, 1989; Mossop & al, 1994
Solanaceae								
<i>Nicotiana tabacum</i> ¹⁶	•	•	•	•	•	•	•	Hill & Malmberg, 1991
<i>Solanum esculentum</i>	•	•	D	•	•	•	•	Bangerth, 1984
<i>S. hirtum</i>	•	D	D	D	•	•	•	Diggle, 1995

¹no unpollinated control; ²basipetal anthesis; ³P:O ratio declines distally; ⁴P:O ratio increases distally; ⁵nectar volume declines distally; ⁶N = 1; ⁷distal flowers lack ovules; ⁸N = 3; ⁹in sage habitat; ¹⁰in forest habitat; ¹¹N = 2; ¹²floral longevity declines distally; ¹³increases distally in small plants, declines distally in large plants; ¹⁴no unpollinated controls, but lack of variation in floral sex allocation among plants that differ greatly in biomass suggests that resources alone are not the cause of positional variation; ¹⁵duration of male-phase decreases distally; ¹⁶inflorescence plastochron interval increases distally.

absence of resource competition from other fruits. A few studies examined variation in both fruit size and fruit maturation. In *Clarkia unguiculata* (Mazer & Dawson, 2001), *Hordeum vulgare* (Cottrell & Dale, 1984), and *Banksia spinulosa* (Vaughton & Ramsey, 1997) both fruit length and fruit production decline distally whereas in *Aspasia principis-sa* (Zimmerman & Aide, 1989), *Polygonatum odoratum* (Gutián & al., 2001), and *Lavendula stoechas* (Herrera, 1991) all flowers have an equal capacity to produce a mature fruit. Those fruits, however, decline in size along the length of the inflorescence. It appears that architectural effects on fruit size can vary independently of effects on fruit maturation.

Thirty-eight studies demonstrated that gynoecium size and/or ovule number vary with flower position on non-fruiting plants. The pattern is predominantly one of proximal to distal decline. Exceptions include *Narcissus dubius* (Worley & al., 2000) in which the distal flower is much larger than proximal flowers, *Maianthemum canadense* (Thomson, 1989) and *Epilobium fleischeri* (Stocklin & Favre, 1994) with a constant ovule number, and *Zigadenus paniculatus* (Emms, 1993) in which the pattern of variation in ovule num-

ber differs with plant size.

In the absence of differential fertilization or ovule abortion, gynoecium size or ovule number should co-vary with fruit length or seed number. In the five studies that examined both ovary and fruit characters the direction of change was the same. In *Lupinus luteus* (van Stevenick, 1957), *Mimulus guttatus* (Macnair & Cumbes, 1989; Mossop & al., 1994) and *Polygonatum odoratum* (Gutián & al., 2001) both ovule number and fruit length or mass decline distally; *Clarkia unguiculata* shows proximal to distal declines in ovule number, and seed number and mass, and in *Hordeum vulgare* gynoecium size at anthesis (there is only one ovule) is closely correlated with mature grain weight and both decline with position on an inflorescence. Thus, it appears that variation in ovule number is likely to affect final fruit size.

Data from four Liliaceous species suggest that positionally based declines in ovule number can have a stronger effect than temporal precedence in determining fruit or seed maturation. *Clintonia borealis*, *Calochortus leichtlinii*, *Erythronium grandiflorum* and *Medeola virginiana* (Thomson, 1989) are characterized by distally declining ovule number but also have basipetal anthesis (distal flowers open first). Although the distal flowers in these species may have been pollinated first and therefore have had a potential temporal advantage in terms of developing sink strength for fruit and seed maturation, seed number per fruit declines acropetally when all flowers are pollinated. These results suggest that positionally determined commitment to ovule primordia during inflorescence development can override the effect of temporal precedence of fruit initiation on seed number per fruit.

Pollen number per anther, anther size, and stamen number commonly decline within inflorescences and eight of eleven studies found that some part of this variation is an architectural effect that occurs independently of fruiting status. One result of changes in pollen and/or ovule number is that the pollen:ovule ratio can vary dramatically among flowers within inflorescences, and seven studies report significant proximal to distal declines in this ratio. The pollen:ovule ratio is often considered characteristic of a taxon and indicative of mating system (Cruden, 1977, 2000; Damgaard & Abbott, 1995).

Corolla size was assessed in 12 taxa and there was significant positional variation in ten. Corolla size typically, but not invariably, was associated with variation in other structures.

Twenty-eight studies examined intra-inflorescence variation in more than one floral character. Of these, the direction of change (increase or decrease) was consistent among all of the characters examined in 14, whereas in the remaining 14 species, there were contrasting patterns of variation. The most common contrast was one in which some organs, or characters, varied while others remained invariant among positions (13 cases). In only one species did some organs show a pattern of decrease while others increased in size with position (*Arabidopsis thaliana*; Diggle, 1997). Positional variation, therefore, can be trait-specific. There is no apparent pattern of which traits tend to vary and which remain constant.

Discussion

The taxa included in this survey represent a broad taxonomic distribution, including a range of eudicots and monocots. Among these disparate taxa, architectural variation is rampant. Of the 112 entries in Table 1, 91 (81%) showed some amount of variation attributable to position alone. Positional variation was documented in all of the floral organ whorls investigated: corolla, androecium, and gynoecium, as well as in pollen and ovule number and fruit and seed characters and maturation. Although proximal to distal declines were the most common pattern of variation, increases were found in many taxa and could occur in any organ whorl. Furthermore, floral organs and characteristics of those organs varied independently of one another. Because of this capacity for independent change in development, particularly in the gynoecium and androecium, the function of flowers can change dramatically within inflorescences.

Consequences of architectural effects for the interpretation of plant reproductive phenotypes. — Architectural effects and intra-inflorescence resource competition. Understanding limits to reproduction has profound consequences for theories and interpretations of the evolution of floral displays and flower characters. For example, the hypothesis that selection on floral traits arises entirely from effects on male fitness assumes that female reproductive success is resource and not pollen limited (e.g., Bell, 1985; reviewed in Campbell & Halama, 1993). Resource limitation is also central to much of sex allocation theory (Charnov, 1979; Charlesworth & Charlesworth, 1987; Campbell & Halama, 1993; Burd, 1999). Thus, it is essential that the occurrence and magnitude of resource effects are identified correctly. Table 1 shows overwhelmingly that architectural variation can mimic the effects of resource competition within inflorescences; proximal to distal declines in floral organ size and fruit size and maturation occur in the absence of resource pre-emption by developing fruit. As a result, the importance and/or magnitude of resource competition as a source of variation in plant reproductive characters has likely been vastly overestimated. To the extent that intra-inflorescence resource competition (e.g., declining fruit set within inflorescences) has been used as evidence for resource limitation of female function, the importance of resources in the evolution of reproductive characters may also have been over-estimated.

Architectural effects and plasticity. Beyond the issue of plastic responses to resource pre-emption by developing fruit, the ability to detect phenotypically plastic responses of flower or fruit characters to environmental variation of any sort potentially is hampered by architectural variation. In light of the importance of reproductive characters in classification/taxonomy and the obvious fitness consequences of floral morphology, it is important to test for plasticity in these characters (Weinig, 2002). Yet, we know little about the occurrence, let alone the fitness consequences, of morphological plasticity of flowers. How plastic are floral and fruit characters? Do floral organs within flowers vary in their plasticity? Is there genetic variation for plasticity of those characters within populations? Do species differ in plasticity? Experimental approaches to these questions depend critically on the ability to distinguish the effects of environmental variables of interest from other factors that underlie phenotypic variation, including positional effects. Examination of flower plasticity in *Arabidopsis thaliana* (Diggle, 1997) showed that

architectural effects can mask plasticity or even alter the perceived direction of plastic response. Similarly, in an analysis of flower plasticity in *Campanula rapunculoides* in response to three environmental variables, Vogler & al. (1999) included flower position as a covariate in the analyses (all plants were left unpollinated, hence fruit set was not a potential source of phenotypic variation). Not only were they able to detect plasticity accurately, but they were able to detect significant genotypic variation for floral plasticity (genotype by environment interaction; Schlichting, 1986). The added power contributed by the inclusion of positional analysis was critical for detecting both plasticity and the genotype by environment interactions. The ability to accurately assess the interactions is particularly important for understanding the evolution of plasticity and the maintenance of genetic variation within populations.

Positional effects may also explain instances where there is an unexpected lack of plasticity. Sargent and Roitberg (2000) predicted that the duration of the male phase of dichogamous flowers of *Epilobium* (= *Chamerion*) *angustifolium* should vary with pollinator visitation. Because visitation rates decline over the season, the male phase duration should increase in distal (later) flowers. In addition, they reasoned that there should be no seasonal (positional) decline in male phase duration when pollinators are prevented from visiting inflorescences. Contrary to prediction, they measured a significant decline in male phase duration, even in plants from which pollinators were entirely excluded. They conclude that “this seasonal pattern may be best explained by some other factor”. That factor may be inherent positional variation in phase duration or flower longevity. A positional decline in male phase duration persists under all experimental conditions despite clear benefits of increasing phase length in the absence of pollinators.

Architectural effects can confound many types of studies. In addition to studies of phenotypic plasticity, architectural variation in floral or fruit traits may confound many other types of studies. For example, positional effects, if unaccounted for, can obscure genetic differences among individuals, families, populations, or species. The work of Mazer and Delasalle (1996) on *Spergularia marina* demonstrates clearly the need to control for positional effects in studies of genetic differentiation among lineages. In *S. marina* most floral traits exhibited significant temporal (= positional) variation, and the magnitude and pattern of this variation differed among populations. For this reason, the ability to detect significant genetic variation among and within the populations was sensitive to the time of sampling, that is, it depended on which flowers were sampled. This study also showed that broad sense heritability estimates, often used in evolutionary genetics to predict potential response to selection, would be sensitive to the position of the flowers measured. An important task of systematic and evolutionary biology is to understand how and why characters differ among lineages. Attempts to characterize population or species divergences, or to measure the extent of genetic variation for traits, must consider architectural variation.

Accounting for flower position also may increase the power to detect trade-offs between male and female function (a common assumption of sex allocation theory; Burd, 1999). If the correlation structure among floral organs changes among flowers within inflorescences, then this variation will confound the precision necessary to measure such trade-offs. Of the nine studies that examined both gynoecium and androecium, seven

report independent variation in these two organ types or report significant increases in P:O ratios with position. Such variation may explain why trade-offs have been very difficult to document at the whole plant level (Burd, 1999).

Explicit inclusion of positional variation into the design of experiments and collection of data can increase precision and power. An equally effective alternative for many studies is to simply control for positional variation, that is, all comparisons and manipulations should be made for flowers and fruits at equivalent positions within the architecture of individual plants. For example, studies of inbreeding often involve comparisons of progeny derived from selfed vs. outcrossed pollinations. In their research on *Mimulus guttatus*, Dudash and colleagues (e.g., Dudash & al., 1997) have determined that these two treatments must always be applied to flowers borne at the same node to control for possible positional effects on fruit and seed characters that may affect progeny performance. Similarly, in their field studies of the effects of density on pollination and reproduction, Bosch and Waser (1999) examined and compared only the basal-most flowers within each inflorescences. Species descriptions in systematic studies and monographs should also include positional information or control for position whenever possible.

In summary, architectural effects are common and can result in a diversity of patterns of intra-inflorescence variation in floral form and function. Because this variation mimics the effects of resource competition in many taxa, any investigation of resource limitation must include an architectural control. More generally, including or controlling for positional variation can add precision to many different types of analyses, including examinations of plasticity, allocation, inbreeding, and even taxonomic circumscriptions. Architectural effects are clearly important for any study of reproductive phenotype, but what are architectural effects?

What are architectural effects? — Architectural patterns of intra-inflorescence variation may be viewed as the result of natural selection and thus may reflect adaptations to differences in mating opportunities and/or resource conditions among flowers at different positions (Brunet & Charlesworth, 1995; Frank, 1987; Burd, 1999; Ashman & Hitchens 2000; Mazer & Dawson, 2001).

Architectural effects may be the result of selection for particular patterns of resource allocation. For example, if as a consequence of resource competition basal flowers always mature fruit and distal flowers rarely do (a plastic response), then natural selection ultimately may result in increased pre-anthesis investment in the ovaries of basal flowers and decreased allocation to distal flowers. The result would be a positional decline in ovary size that is expressed regardless of the current fruiting status of the individual plant or inflorescence (an architectural effect). Ashman and co-workers provide evidence for such an evolutionary scenario in *Fragaria virginiana*, the wild strawberry. This species is gynodioecious, and populations consist of females, hermaphrodites, and functional males (morphological hermaphrodites that rarely set fruit). All three morphs show dramatic declines in ovule number per flower within inflorescences, and this pattern is expressed identically in both fruiting and non-fruiting plants; the decline in ovule number is strictly a positional effect (Ashman & Hitchens, 2000). The positional effect, however, differs among the sex morphs. Females invest most heavily in gynoecia of flowers in first positions, and ovule number declines rapidly in distal flowers. It appears that flowers with the

greatest probability of setting fruit have been provisioned with the most ovules. In contrast, functional males (in which fruit set is rare at all flower positions) invest far less in gynoecea at first positions and exhibit lower decrements in ovule number over the inflorescence compared to females. Thus, the differences between the sex morphs in the pattern and magnitude of positional variation among flowers may be the result of past selection for differences in ovary function (Ashman & Hitchens, 2000). While resource competition is not the proximate cause of positional variation, it may be the ultimate cause.

In the example of *Fragaria*, female function declines predictably with position. More generally, relative male and female reproductive success may differ among flower positions within inflorescences, and floral sex allocation might vary accordingly. Mazer and Dawson (2001) have argued that sex allocation theory developed for whole organisms (Charlesworth & Charlesworth, 1981, 1987; Charnov, 1982; Lloyd, 1984; Lloyd & Bawa, 1984; Geber & Charnov, 1986; Charlesworth & Morgan, 1991; Spalik, 1991) can also be applied to individual flowers (see also Brunet & Charlesworth, 1995; Burd, 1999). As in whole plant models, a trade-off between investment in male vs. female function per flower is assumed: controlling for resource status, flowers producing relatively large amounts of pollen must produce relatively few ovules or seeds. If flower resource status decreases predictably with position, then successively produced flowers should become more male-biased. That is, there should be a proximal to distal progression of floral gender from female to male-biased flowers.

Positional variation in relative allocation to female and male function also may arise from selection by pollinators that habitually visit inflorescences in an acropetal pattern (Brunet & Charlesworth, 1995). The first flowers visited will receive more pollen from other plants (will be more outcrossed) than will flowers that are visited subsequently, and the last flowers visited will be the most successful at exporting pollen to other plants (Robertson, 1992; Barrett & al., 1994; Harder & Barrett, 1995; Vogler & al., 1999; Harder & al., 2000; Aizen, 2001; Kudo & al., 2001; Ishi & Sakai, 2002). Thus, the contributions of male and female functions to reproductive success are expected to differ between flower positions within inflorescences, and floral sex allocation may vary accordingly. That is, proximal flowers will have greater allocation to female function while allocation to male function will increase distally.

The many studies that show declining ovule number, increasing pollen production, or increasing P:O ratios with position are consistent with either of the two models for the evolution of intra-inflorescence gender variation. However, many other patterns are documented in Table 1 and “adaptive” hypotheses for these patterns have not been formulated.

Although some types of positional variation in morphology or function clearly may be the result of natural selection, such hypotheses depend implicitly on the pre-existence of some kind of positional information within inflorescence axes. In order for intra-inflorescence diversification of, for example, floral gender to evolve, there must be a gradient or signal that elicits differential development of floral organs according to the positional context of the flower. Thus, although positional variation in morphology and function may, in some cases, be the result of natural selection, selection requires underlying positional information or developmental cues to generate predictable intra-inflorescence vari-

ation in reproductive phenotype; natural selection can only act on existing variation. Therefore, a complete answer to the question “what are architectural effects?” requires the identification of a proximate developmental cue.

One hypothesis for a proximate cue is that architectural variation is just resource competition occurring earlier in development than the fruiting stage. That is, variation in morphology or function among flowers of non-fruiting plants occurs because resources will always be consumed during the developmental process and later, distal, flowers will always be at a disadvantage with respect to resource allocation. Resource level within inflorescences as a proximate explanation for intra-inflorescence variation is only viable if the predominant pattern of variation is one of proximal to distal declines in all floral organs. Table 1 shows that while proximal to distal declines are common, there are multiple examples of patterns of increase and of taxa in which the pattern of variation differs among the four organ types. It is difficult to explain how floral organs respond to resource limitation by increasing in size or how two different floral whorls respond to the same resource gradient differently. Such complex patterns of variation argue for an alternative proximal explanation.

A second hypothesis is that architectural effects are attributable to declining amounts of vascular tissue along the length of an inflorescence (Wolfe & Denton, 2001). The same complex patterns of intra-inflorescence variation that argue against resource variation also indicate that vascular supply may not provide a universal explanation. In addition, vascular differentiation is clearly plastic and responds to the demands of developing sinks such as flowers and fruits (Gifford & Evans, 1981; Uma Shaanker & al., 1988; Ganeshiah & Uma Shaanker, 1994; Bustan & al., 1995). Inflorescences are likely to contain the amount of vascular tissue necessary to supply the demands of distal structures.

Resource competition and declining vascular supply are not likely general explanations for the patterns of intra-inflorescence variation summarized in Table 1. Furthermore, many other types of intra-inflorescence variation also require the existence of positional information or gradients. For example, in many monoecious (including andromonoecious and gynomoecious) taxa, female and male flowers occur within the same inflorescence in highly characteristic and predictable locations (e.g., Waller, 1988; Waller and Steingraber, 1995). Similarly, in highly syn-organized inflorescences such as those of *Hydrangea*, *Cornus*, and Asteraceae, flowers at different positions have highly divergent morphologies and functions. Resource gradients or vascular supply cannot easily account for this type of variation. An explanation of architectural effects should be general enough to explain diverse manifestations of intra-inflorescence variation.

Although a mechanistic explanation of architectural effects is not at hand, there are clearly positional cues or gradients of some sort that exist within the reproductive axes of flowering plants. In most taxa these gradients result in subtle quantitative variation in form or function of the type summarized in Table 1. In other taxa, however, these gradients may provide the positional information necessary for qualitative divergence in form and function that result in the evolution of monoecy or other types of intra-inflorescence dimorphisms. Thus, architectural effects themselves are important and interesting morphological features that require more study. Understanding architectural effects may lead to insights ranging from understanding controls of morphogenesis to evolutionary diver-

sification of flowers within inflorescences.

Conclusions. — In summary, while the number of studies that explicitly examine positional variation among flowers within inflorescences is increasing, more are required. There are still too few data to begin asking about such issues as the phylogenetic distribution of architectural effects or the association of positional variation with other plant traits such as life history, growth form, inflorescence type, mating system, or particular flower morphologies or fruit types. Clearly, however, the research summarized here demonstrates that the default assumption that all flowers and fruit have similar developmental potentials is in error. Architectural effects are a common and important component of plant reproductive phenotypes and understanding positional variation is critical to many different areas of plant reproductive biology. Accounting for architecture adds precision to studies in areas as diverse as population genetics, phenotypic plasticity, and taxonomic circumscriptions. Furthermore, investigations of the proximate controls of architectural variation is likely to lead to new insights in the control of floral morphogenesis and to models for the morphological and functional divergence of flowers within inflorescences.

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