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short note

DEPLOYMENT OF OVULES AND POLLEN AMONG FLOWERS WITHIN INFLORESCENCES

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Darwin (1877) devoted a book to the significance of 'The different forms of flowers on plants of the same species', thereby stimulating a century of research into the function and evolution of such differences. Such research, however, has concentrated on obvious, qualitative differences such as chasmogamy vs cleistogamy, staminate vs pistillate vs perfect flowers, heterostyly, etc., and has paid much less attention to quantitative, continuous differences among perfect flowers within plants. (A notable exception is the pioneering treatment of *Muntingia calabura* by Bawa and Webb (1983).) In a largely separate line of research, considerable attention has been paid to pollen: ovule ratios, as indices of phenotypic gender or as correlates of the mating system (e.g. Cruden, 1977). Pollen:ovule ratios, however, have usually been treated as a stable characteristic of the species in question; variation among plants, or among flowers within inflorescences has been virtually unstudied, presumably due to the tedium of counting pollen grains. (Indeed, the few studies that are exceptions have used electronic particle counters (Harder *et al.*, 1985; Devlin, 1988; H. Young and M. Stanton, unpublished manuscript, but see Bawa and Webb, 1983; McKone, 1987).)

Probably because of the lack of data, there is little theory that addresses the question of why pollen and ovules might not be deployed equally among hermaphrodite flowers of a multi-flowered plant. Lloyd and colleagues (e.g. Lloyd, 1980; Lloyd *et al.*, 1980) have proposed a 'hypothesis of serial adjustment of maternal investment' that does consider how the reproductive effort spent on earlier flowers might affect the provisioning of later flowers. Under this hypothesis, for example, ovule number in later flowers might be adjusted downward if the earlier flowers had set exceptionally heavy seed crops. In contrast to adjustments of this sort, which can be thought of as tactical responses to environmental contingencies, there may also be more 'strategic' patterns of pollen and ovule deployment among flowers— patterns that are fixed before flowering begins. One extreme case is described by Holtsford (1985) for two-flowered plants of *Calochortus leichtlinii*, in which the second flower has far fewer ovules than the first. The situation in *Muntingia calabura* seems to fall between these extremes: pistil size increased in later flowers after earlier buds were removed, but stamen number showed no response, presumably because the stamens had already been differentiated (Bawa and Webb, 1983). Here, I survey a number of few-flowered liliaceous geophytes that, like *Calochortus*, produce a single inflorescence with a predetermined number of flowers, opening more or less sequentially. Because such plants typically bloom immediately after breaking the ground, I assume that ovule and pollen numbers are determined for all the flowers before the first flower opens; this is certainly the case in *Erythronium* (personal observation; B. Carr, personal communication). Most of the data concern ovule number patterns, but I present pollen data where available. For several of the species, sample sizes are small, and I present these preliminary data primarily to stimulate new hypotheses and more data collection, rather than as a complete description of the phenomena involved. Even so, robust patterns emerge across species, and the detailed patterns found in *Erythronium grandiflorum* may serve as a basis for future comparisons.

An informal survey of 13 native and one naturalized species from North America and Australia reveals that ovules per flower commonly decline in successively opening flowers within the inflorescence (Table 1). This occurs whether or not the blooming sequence is acropetal or basipetal. In extreme cases (*Brodiaea*, *Bulbine*, *Wurmbea*; also some *Lilium* cultivars), the last flowers have no gynoecium; thus the plants are technically andromonoecious, although seldom described as such. The decline in ovule numbers appears to be associated with a lower probability of fruit set in later flowers. Among the species treated here, later flowers of *Calochortus leichtlinii* (Holtsford, 1985), *Clintonia borealis* (also see Galen *et al.*, 1985), *Medeola virginiana* and *Erythronium grandiflorum* are less likely to be successful (Fig. 1). Holtsford (1985) cites similar results

Table 1. Ovule and pollen deployment patterns in various Liliaceae

Species	Fls/infl	Sequence	Typical maximum ovule no.	Declining ovule numbers	Increasing P/Os
Bulbine bulbosa	4−6	a	30	3/3	3/3
Burchardia umbellata	5	w	60	3/3	−
Brodiaea douglasii	10	a	36	1/1	1/1
Calochortus gunnisonii	2	b	105	10/10*	5/10
Calochortus leichtlinii	2	b	95	see caption*	−
Chamaescilla corymbosa	5	a	18	2/3	−
Clintonia borealis	5	b	18	10/10*	−
Convallaria majalis	6−7	a	15	2/2	
Erythronium grandiflorum	2−3	b	100	81/91*	58/90*
Fritillaria pudica	2	b	110	3/3	−
Maianthemum canadense	6	a	4	invariant	1/2
Medeola virginiana	3	b	16	10/12*	−
Polygonatum pubescens	3	a	12	2/2	−
Uvularia grandiflora	2−3	b	30	2/2	1/1
Wurmbea dioica	4	a	80	10/10*	10/10*

The values for flowers per inflorescence represent the material examined here, not necessarily species characteristics. Blooming sequence codes are: a, acropetal (i.e. basal flowers open first); b, basipetal; and w, whorled, all flowers arise at the same point. For each inflorescence, I determined whether ovule numbers increased or decreased, i.e. I examined the sign of the slope of a regression of ovule numbers on flower opening sequence. The column 'declining ovule numbers' gives the number of plants with negative slopes/the number examined. Holtsford (1985) does not present data for *Calochortus leichtlinii* in the form used here, but reports a very strong decline in ovule numbers: first flowers, $\bar{x} = 96.0$, s.d. = 10.3; second flowers, $\bar{x} = 51.6$, s.d. = 4.9; n = 20 for each. Significance tests for the slopes are not presented; in most cases, there are too few flowers per inflorescence for tests within inflorescences, and too few samples within a species for tests at that level. However, the preponderance of declining slopes is highly significant ($p < 0.001$) at the species level, by a sign test: only the invariant *Maianthemum* does not decline, on average. Asterisks indicate significant ($p < 0.05$) declines within species, based on χ^2 goodness-of-fit tests. The last column examines sequence patterns of pollen:ovule ratios, based on electronic particle counter counts of pollen. In *Bulbine bulbosa*, *Brodiaea douglasii* and *Wurmbea dioica* the last flowers lack ovules altogether. Of the remaining species, *Erythronium grandiflorum* shows a significant pollen:ovule increase, *Calochortus gunnisonii* shows no pattern, and the others lack sufficient sample size.

from seven genera in other families; J. Brunet (personal communication) confirms the same pattern for *Aquilegia caerulea*; Bawa and Webb (1984) also document cases, and provide some review. Possible reasons for late-flower failure include a lower probability of pollination (but see Thomson, 1985), an increased frequency of geitonogamy, greater herbivory, or interfloral competition for fruit-developing resources (see Stephenson, 1981). Although any of these might apply in any particular situation, the near-ubiquity of the declining ovule pattern argues for the least system-specific explanation, i.e. the resource competition hypothesis. With particular reference to this group of plants, the resource competition hypothesis is supported by experiments in *Calochortus* (Holtsford, 1985), *Erythronium* and *Clintonia* (Table 2), in which prevention of fruit set in early flowers increased seed or fruit set in later ones. Thus, later flowers have the potential for full female function, but seldom display it.

Bawa and Webb (1983, 1984) and Holtsford (1985) discuss various possible explanations for the retention of late flowers that have a lower expected seed output; one likely factor is that such flowers contribute to fitness through male function. Bawa and Webb (1983) showed dramatic increases in stamen number in later flowers of *Muntingia calabura*; where stamen number is fixed, counting pollen grains can further clarify the male function hypothesis, testing whether later flowers should retain high pollen production, or even show phenotypic specialization for male function. In some species (Table 1) pollen:ovule ratios do increase in later flowers, indicating sex-differential deployment of resources at anthesis, or phenotypic sex-role specialization. Thus, ovules do not decline simply through later flowers being miniature copies of earlier ones; rather, male and female gametes follow different allometries (but see Arnold (1982) for a report of no pattern in *Linaria vulgaris*). Of course, whether later flowers are actually more *successful* through male function depends largely on the availability of mates (phenotypic vs functional gender; Lloyd, 1980; Thomson and Barrett, 1981). (Clearly, the last flowers

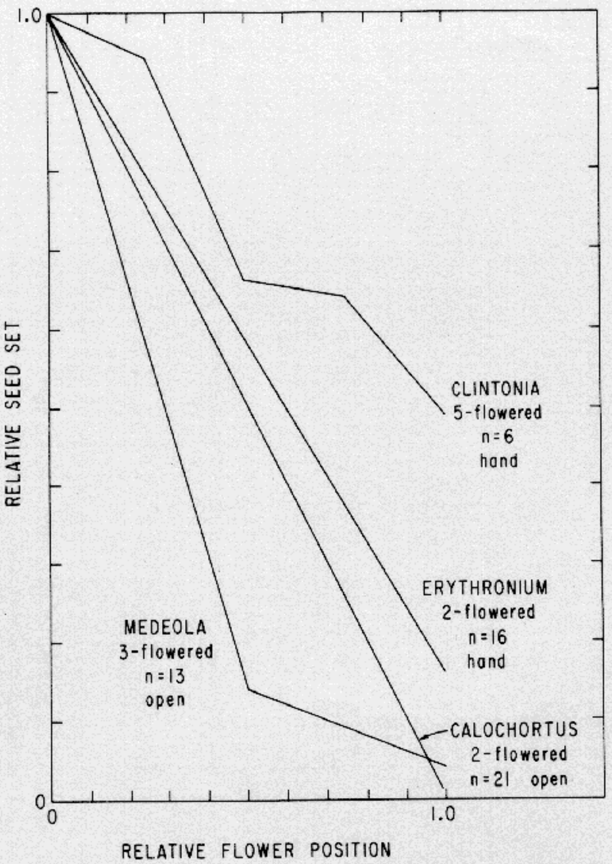

Fig. 1. Relative seed set as a function of flower opening sequence in four Liliaceae. Only inflorescences in which at least one flower set fruit are considered. Relative seed set is calculated as the ratio of seeds/ovules for a flower, divided by the ratio of seeds/flower for the first flower. In *Clintonia* and *Erythronium*, all flowers were hand pollinated; *Medeola* and *Calochortus* (Holtsford, 1985) were open pollinated. Fruit abortions, which are included as zero seed sets, occurred in all species; virtually all second flowers abort in *Calochortus*.

of the andromonoecious plants retain *only* male function.)

Developing a comprehensive theory of pollen and ovule deployment (including both strategic and tactical aspects) will require much more descriptive information and much more refinement of hypotheses and experiments (Thomson, 1985; Pellmyr, 1987). The increasing availability of electronic particle counters should be a stimulus for counting pollen. However, a focus on pollen and ovule numbers should not be allowed to obscure the existence of exactly analogous variation at other levels (e.g. stamen number; Willson and Schemske, 1980; Bawa and Webb, 1983). Similarly, the better-developed theory on qualitative variation among flowers within plants (see especially Lloyd and Bawa, 1984) should be considered of great relevance to explanations of quantitative variation.

Table 2. Effects on seeds per fruit of competition for resources among flowers within inflorescences

1. *Erythronium grandiflorum*, 3-flowered inflorescences, Colorado, 1986

	All flowers pollinated	Only first or last pollinated	F for treatment effect
First flower	42.0 (26)	47.5 (28)	1.72 ($p=0.2$, n.s.)
Last flower	33.9 (29)	41.2 (30)	3.89 ($p=0.05$)

2. *Clintonia borealis*, 5-flowered inflorescences, New Brunswick, 1980

	All flowers pollinated	Only first or last pollinated	Mann–Whitney U_s for treatment effect
First flower	15.8 (11)	15.1 (7)	39.52 ($p > 0.5$, n.s.)
Last flower	5.6 (5)	13.9 (7)	35.0 ($p < 0.005$)

The experiments had three treatments: (1) all flowers pollinated, sequentially as they opened; (2) only the first flower pollinated; (3) only the last flower. The tabled entries are: number of seeds (sample size). Higher competition (the 'all flowers pollinated' treatment) does not diminish seed set in the first flower, but does in the last flower. Complete abortions of fruits are included as 0 seed set, although there were few abortions in these experiments. In both species, abortion is common in other circumstances (personal observation; Cruzan and Thomson, in preparation).

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