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POLLINATION AND SEED SET IN DIERVILLA LONICERA (CAPRIFOLIACEAE): TEMPORAL PATTERNS OF FLOWER AND OVULE DEPLOYMENT[1]

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ABSTRACT

Ovule development in *Diervilla lonicera* (Caprifoliaceae) is limited by insufficient pollination early in the blooming period and during extensive rainy periods. Production of flowers is skewed in time; an initial burst of flowering is followed by a long period of sparse flower production. Ovule number per flower increases through the blooming period. I discuss the interactions of fruit and seed set, ovule number, and bumble bee pollinator visitation patterns. When certain flowers have a higher a priori probability of successful pollination, it may be advantageous for plants to put more ovules in those flowers. Selective ovule deployment may be a general adaptive phenomenon that has received little attention.

THE "FLOWERING CURVE" of a plant population, by which is meant a graph of the numbers of functioning flowers vs. time, has been a concern of evolutionary ecology for some time. Most attention has been paid to the relative timing of flowering curves of plant species that might interact with each other (reviewed by Rathcke, 1983, and Waser, 1983). In addition, the shapes of flowering curves for plant populations have also received some attention (Thomson, 1980, 1982, 1983). However, little has been published about the timing of flower production in individual plants that produce many flowers, or about the distribution of ovules among flowers in cases where ovule number varies. In this paper I describe the temporal presentation of flowers and ovules in a clonal patch of the self-incompatible entomophilous shrub *Diervilla lonicera* Mill. (Caprifoliaceae). I then overlay the temporal pattern of successful seed set, and finally discuss aspects of pollination ecology that may act as selective forces in the evolution of flower and ovule deployment patterns.

MATERIALS AND METHODS—A discrete subpopulation of *Diervilla lonicera* was studied ~5 km SE of Doaktown, New Brunswick during June–August 1979. The patch comprised ~70 blooming stems within ~15 m^2. The plants were located at the edge of a rarely used logging road in disturbed spruce-fir forest; other patches of *Diervilla* were located along the road, but the study patch was separated from the other patches by at least 20 m. Schoen (1977) describes the floral biology of this species in detail.

Before flowering began, a stratified random sample of shoots with buds was chosen by dividing the patch into a 5 × 5 grid and selecting the stem nearest a randomly chosen point within each grid cell. One additional stem was randomly chosen in a peninsular clump of stems outside the grid.

Each day during anthesis, the 26 stems were inspected for flowers. All flowers were individually tagged, using a 2.5 × 20 mm white self-adhesive paper label folded over on itself around the flower stalk. Bud break, flower opening, anther dehiscence, and wilting were recorded. Most flowers opened fully, were receptive, and bore nectar on the same day as bud break. In a minority of flowers, one or more anthers dehisced on the first day, but dehiscence was usually delayed until the second day of bloom. On the third day most flowers wilted and the corollas dropped. The flowers were examined in the afternoon, and a flower was scored on the day when it first opened fully. Each flower was counted on only one day, although most had a two-day life. After flowering, fruits were harvested at a stage when developed and undeveloped ovules could be counted under the dissecting scope. The fraction of ovules developed was computed; damaged fruits were excluded. No attempt was made to distinguish between unfertilized and aborted ovules.

In June 1980 the patch was partially excavated in an attempt to determine the extent of

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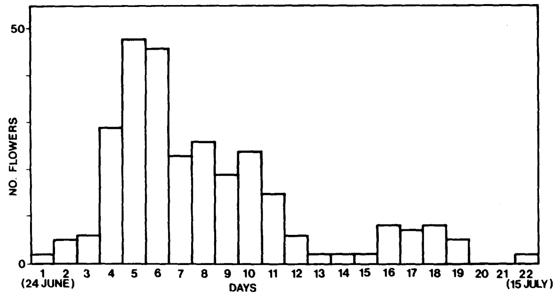

Fig. 1. The flowering history of a sample of 26 shoots within a putative clone of *Diervilla lonicera*. The mean date of flowering is 8.05 days after 24 June; the skewness g_1 = 1.20.

underground connection between shoots. The results were somewhat equivocal. Although many of the shoots were connected by rhizomes, some appeared to be isolated. It was impossible to determine whether the apparent isolates had once been connected to the others by rhizomes that had subsequently rotted or been severed. This discussion will generally assume that the patch of *Diervilla* is a single clone, although the possibility does exist that several genotypes may be represented.

Meteorological data for Doaktown were supplied by the Atmospheric Environment division of Fisheries and Environment Canada and supplemented by field notes.

RESULTS—*Summary data for the subpopulation sample*—The flowering curve for the sample (Fig. 1) is positively skewed. Using Sokal and Rohlf's (1981) formulae for grouped data, the skewness $g_1 = 1.20$, which represents a highly significant departure from symmetry about the mean ($N = 285$ flowers, $P[g_1 = 0] < .001$). The distribution is also leptokurtic ($g_2 = 3.95$, $P[g_2 = 0] < .001$). Using the numbering convention adopted in Fig. 1, the mean time of flowering is 8.05 days after 24 June.

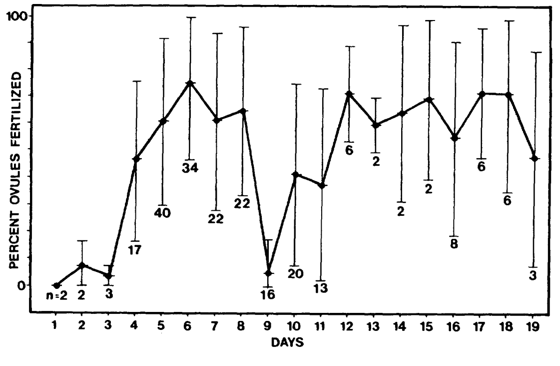

Fig. 2. The female "success curve" for the sample, i.e., mean percentage of ovules developed (± 1 SD) versus time. The number of flowers used to calculate the means are displayed for each day.

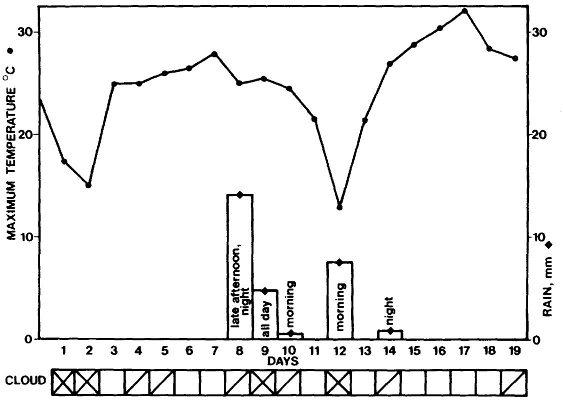

Fig. 3. Weather data. Maximum daily temperature is represented by the upper line, rainfall by the vertical bars. The times of rainfall are given. A single slash indicates partly cloudy conditions; a double slash, full overcast.

The fraction of ovules matured is plotted against time in Fig. 2. Seed set is initially low but rapidly rises to a plateau, with the exception of the great depression at Day 9. This decrease is probably due to fewer pollinator visits during a long rain on Day 9 (2 July; Fig. 3). Other rainy periods during the flowering period were of shorter duration or nocturnal and had less effect on seed set. Temperature and cloudiness appeared to be uncorrelated with fertilization percentage.

The number of ovules per flower is highly variable, with a range from 9 to 55 and a mean and standard deviation of 28.34 and 9.51. Figure 4 graphs the mean number of ovules per flower as a function of the day of bloom. Mean ovule number increases significantly ($P < .05$) with time. Both of the two recorded components of herbivorous damage to flower and fruits, which included grazing of entire flowers or fruits and attacks of dipteran larvae on developing fruits, are rare and uncorrelated with time.

Patterns within shoots—In Table 1, the overall flowering curve is broken down into the contributions of the 26 individual shoots. Although there are few flowers per shoot, there is a tendency towards positive skewness (19/26 cases) and in some of the shoots with larger numbers of flowers, the skewness is significant. Table 1 shows that the skewness seen in the overall flowering curve for the patch has two components: most shoots begin flowering early, and each shoot tends to produce most of its flowers early.

TABLE 1. *Temporal patterns of flower production on 26 shoots of a putative clone of* Diervilla lonicera. *Asterisks indicate that the observed degree of skewness of the flowering curve deviates significantly from a symmetric distribution (* = P < .05, ** = P < .01). Day 1 corresponds to 24 June*

Flowering shoot	Days 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	Mean day of flower production	Skewness (g_1) of the flower curve
A	2	5	1																				1.88	.054
B				2	8	3	1	2															5.56	.901
C						4	2	0	0	1													6.86	1.637*
D							3	0	0	2	1	1											9.14	.028
E					2	5	2	4	2														6.93	.124
F						2	1	0	0	1	1												8.20	.545
G					3	5																	5.62	−.516
H									2	4	3	1	0	0	1	0	2						12.00	.819
I						2	3	1	0	1	1	0	0	0	0	0	0	0	0	0	0	2	10.60	1.269
J						2	0	2	0	2	1	1											8.87	−.081
K							2	2	5	3	2	2	0	0	0	1	5	1	3				12.58	.314
L								3	1	2	0	0	1	1	0	1							10.67	.714
M								2	4	6	2	0	0	0	0	3							10.71	1.308**
N				2	5	3	2	2	0	0	1												6.13	1.208*
O			2	0	0	4	1	1	2														6.30	−.341
P				3	3	2	2																5.30	.289
Q				5	5	5	0	1	1														5.41	1.136*
R				7	12	0	1	0	0	0	1	0	1										5.32	2.425**
S				5	0	6	1	4	1	0	2												6.63	.512
T			3	3																			3.50	0.000
U					4	0	2																5.67	.707
V					1	3	0	0	1														6.40	1.173
W															1	1	0	3	2				17.57	−.772
X								2	0	1	1												9.25	.214
Y				2	5																		4.71	−.949
Z													1	1	0	2	0	4					16.38	−.668

DISCUSSION—*Pollinator visitation and seed set—Diervilla lonicera* in New Brunswick is visited primarily by *Bombus vagans,* a bumble bee that is especially active in forest understory and that has been shown to "trapline"—i.e., to visit particular plants in more or less repeatable sequences—in certain circumstances (Thomson, Plowright and Maddison, 1982). The observed pattern of low seed set for the first few days of flowering, followed by a rapid rise (Fig. 2), may reflect a low initial visitation rate until a sufficient number of bees located the new patch and incorporated it into their foraging circuits. The sharp depression of seed set on Day 9, coinciding with all-day rain, also suggests limitation by pollinator activity.

Components of pollination success and optimal flower and ovule presentation schedules—Diervilla lonicera plants exist as widely spaced patches in the forest. To the extent that patches are clonal, successful seed set requires that compatible pollen be imported from other patches. The earliest flowers on a plant are likely to suffer from inadequate pollination because pollinators have yet to discover the plant; there is an advertising cost (Thomson, 1982). In such circumstances, there are two separate means by which a flower contributes to the fitness of the plant that produced it: first, the straightforward contribution of gametes to the next generation; second, pollinator familiarization and recruitment, whereby early flowers increase visitation to later flowers produced by the same plant. The balance between these fitness contributions shifts during the blooming period, with the early flowers bearing the brunt of the advertising contribution.

When pollinators respond preferentially to concentrations of bloom and show site fidelity, a positively skewed flowering curve may be the optimal deployment of flowers for an individual plant (cf. Thomson, 1980). By presenting a large number of flowers initially, the plant may obtain the services of faithful visitors that will continue to visit despite subsequent decreases in the rate of flower production. The pollinations obtained late in flowering are less likely to be geitonogamous than those from the peak flowering period.

An alternative hypothesis is that the shape of the flowering curve of a plant has no adaptive significance but is merely a product of unspecified physiological or morphological con-

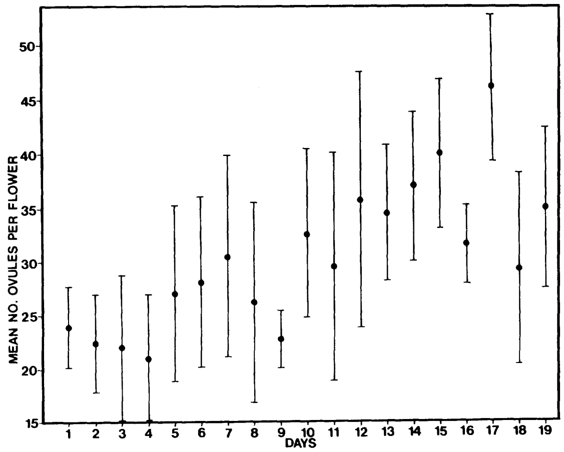

Fig. 4. The mean number of ovules per flower vs. time, ±1 SD. Sample sizes for each day are the same as those given in Fig. 3. The product-moment correlation between mean number of ovules per flower and time is significant ($r = .45$, $df = 17$, $P < .05$).

straints. The only ways of evaluating such hypotheses are by performing selection experiments or by comparing flower presentation patterns in related plants with different pollination systems. However, there is another line of evidence suggesting that flower presentation in *Diervilla lonicera* may indeed reflect the uncertainty of pollination of earlier flowers. This is the tendency for ovule numbers per flower to increase with time (Fig. 4). If early flowers are necessary for pollinator attraction but are unlikely to be visited, it would be more economical to invest few ovules in them. Early flowers might also produce more pollinator rewards, as befits their primary role in securing site-faithful pollinators. This prediction remains untested.

The deployment of ovules across flowers within an inflorescence or a plant has received little attention. In several monocot genera (*Narcissus, Clintonia, Erythronium, Medeola*) there is a tendency for later flowers in an inflorescence to have fewer ovules, the opposite pattern of that shown in *Diervilla* (Thomson, unpub. data). I know of no other data. At first glance, the lily pattern seems easily explicable as a simple physiological result; the last flowers may have fewer ovules as a consequence of resource exhaustion. However, in these plants the flower buds, including ovules, appear to be completely differentiated underground long before blooming begins. If the lesser complements of ovules in later flowers are due to resource depletion, it must take place as the buds develop during the previous season.

In *Clintonia* at least (Galen, Plowright and Thomson, 1985) the later, fewer-ovuled flowers are more likely to abort, just as in *Diervilla* the *earlier,* fewer-ovuled flowers are more likely to abort. It would be very interesting to know if a general principle links ovule number and the probability of successful fruit set, and if so, to know the direction of causality. Plants may selectively abort flowers that have had a small number of ovules fertilized (Lee and Bazzaz, 1982; Stephenson and Bertin, 1983). In circumstances where the failure of certain flowers (e.g., early or late ones) is somewhat predictable, plants may also adjust ovule numbers to maximize fitness returns on a fixed investment of resource. Much more work will be necessary to test this conjecture. Given the ease of counting ovules, and the noteworthy variation in ovule numbers within and between plant families, and within and between multiflowered individual plants, it seems that a comprehensive theory of ovule number is overdue (although Kress, 1981, and Willson and Burley, 1983, have provided some provocative starting points).

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