

The Effect of Pollinators, Predators, and Energy Constraints on the Floral Ecology and Evolution of *Trillium erectum*

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Summary. The reproductive success and energy budgets of single and multiflowered plants of *Trillium erectum* L. (Liliaceae) were assessed over a period of 4 years. Plants with more than one flower were found to attract more pollinators, to be less vulnerable to predation by Tortricid moths, and to produce more seeds than single flowered plants. Despite the reproductive superiority exhibited by multiflowered plants, most plants (85%) in the population studied were single flowered. It is shown that even though the insect interactions make it advantageous to produce more than one flower, most plants lack the energy to do so. The optimality approach which has guided previous studies of this kind is criticized.

Introduction

By producing more flowers, a plant may attract more pollinators (Willson and Rathcke 1974; Willson and Price 1977) and produce more seeds (Schemske 1980; Zimmerman 1980). However, in becoming more conspicuous to pollinators, a plant may also increase the likelihood of detection by flower and seed predators (Beattie et al. 1973). Moreover, the production of additional flowers may exact such a high energy cost that survivorship and future reproduction may be jeopardized (Williams 1966).

Assuming that the evolution of floral displays represents a compromise between a number of such conflicting pressures, previous investigators have chosen an optimality approach to understanding inflorescence production (Willson and Price 1977; Willson et al. 1979; Schemske 1980). In these studies, it was predicted that the optimal phenotype, the floral display that produced the most seeds and attracted the most pollinators, would be the most common phenotype. However, in most cases the optimal floral display was found to be much larger than that exhibited by the vast majority of plants. This forced the investigators to try to reconcile the disparity in some way, either by suggesting that many plants are "mistakes" (Willson et al. 1979), that the smaller inflorescence must be optimal in some other way (Willson and Price 1978; Willson et al. 1979; Schemske 1980), or that many plants are unable to produce the large floral displays due to energy constraints (Willson and Rathcke 1974; Willson and Price 1980). Unfortunately, the lack of pertinent data thus far has precluded the evaluation of any of these hypotheses.

This paper reports on a study of the floral display of *Trillium erectum* L. (Liliaceae) in which the energy budget and the repro-

ductive success of the plants were assessed. The paper compares the abundance with the reproductive success of single and multiflowered plants of *Trillium erectum* L., and examines the relative merits of an optimality and an energy budget interpretation of the findings.

The Plant and Its Fauna

T. erectum is an herbaceous spring perennial which grows in rich woods from southern Canada, New England, New York and Pennsylvania, to as far south as the mountains of Tennessee and Georgia (Fernald 1950). In most populations, there are single flowering and multiflowering plants, as well as younger plants that are nonflowering. In multiflowered plants, each flower arises from a separate stem which originates from the rootstock (Fig. 1).

Dyer (1963) reported that *T. erectum* is self sterile, however Ihara (1973) has cited some problems with Dyer's work, and he and Patrick (1973) in separate studies, have been successful in effecting self pollination. When outcrossing does occur, it is accomplished primarily by dipterans (including Anthomyiidae, Sciaridae, and Sarcophagidae) which are probably attracted by the fetid odor produced by the flowers (Weed 1895; Robertson 1896, this study).

In New Hampshire, the flowers are frequently infested by the larvae of 2 species of Tortricid moths, *Clepsis persicana* (Fitch) and *C. melaleucana* (Walker). The *Clepsis* moths are relatively northern species found in boreal habitats over much the same range as *T. erectum* – Quebec, Ontario, Nova Scotia, New England, New York, Pennsylvania, and in the case of *C. melaleucana*, as far south as the mountains of North Carolina (Chapman and Lienk 1971). These moths are univoltine and they utilize woody plants as primary hosts. Eggs are laid in June and the larvae have been found on a number of trees, including *Populus tremuloides*, *Picea alba*, *Salix spp.*, and *Betula papyrifera*. The larvae emerge later in the summer and feed on their woody hosts. After dropping to the forest floor, the larvae overwinter in the litter as 5-th or 6-th instars. In the spring, they complete their development on secondary hosts, which frequently are herbaceous. The larvae have been found feeding on a wide variety of herbaceous plants, including, *Ranunculus*, *Solidago*, *Polygonatum*, and *Taraxacum* (*Clepsis* life history information from Chapman and Lienk 1971). When the larvae infest *T. erectum*, they bind up the flowers and completely devour the stamens and ovary.

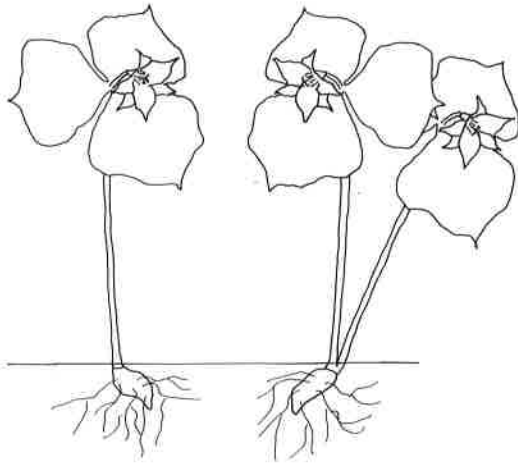


Fig. 1. Drawing of a single flowered and double flowered plant of *Trillium erectum*

Study Site

The study site consisted of a 1 hectare plot in the Hubbard Brook Experimental Forest near West Thornton, New Hampshire. This is a northern hardwood forest dominated by *Fagus grandifolia*, *Betula lutea*, and *Acer saccharum*. The understory comprises *Acer pensylvanicum*, *Acer spicatum*, and *Viburnum alnifolium*. Herbs, tree seedlings, ferns, and mosses compose the flora of the forest floor.

Methods and Materials

Flower predation was assessed during May in 1977 ($N=196$), 1978 ($N=837$), and 1980 ($N=200$). In 1978 and 1980, the respective infestation rates of single and multiflowered plants was also recorded. The figure for 1978 (837) represents a census of all the flowers on the study plot, while in other years, the population was sampled randomly.

During May 1979 visitation rates of dipterans were assessed by spreading a thin film of a sticky substance, *Tanglefoot*, on flowers of both single and double flowered plants. Flowers were collected 4 days after they had been covered with *Tanglefoot* and the number of flies that had become mired were counted. In June 1979, single, multiflowered, and nonflowering plants were collected and the dry weight of their constituent parts – rootstock, stem, leaves, and flowers – was measured using a Mettler balance. The number of nodes, or “annual constrictions” (Brandt 1916, see Fig. 2) on each rootstock was also recorded, along with the mean width of the internodes, which was calculated by measuring the length of the rootstock with a micrometer, and dividing the length by the number of nodes. These data were taken to provide estimates of the age and of the average yearly growth of the plants (Brandt 1916).

In June 1979, the location of 128 plants was marked by placing a wire stake with flagging into the ground next to each of the plants. In May 1980, these plants were checked and their flowering state noted.

Ovule production and seed set was determined in single flowered plants from flowers collected and dissected in 1978, 1979, and 1980, and in double flowered plants from flowers collected in 1980. Owing to the large number of ovules produced by many flowers, (as high as 200 or more), one of the locules was arbitrarily selected and only those seeds contained in it were counted.

Results

Census

A total of 707 *Trillium* plants were found in flower on the study plot in 1978. Of these, 107 (15.1%) produced more than

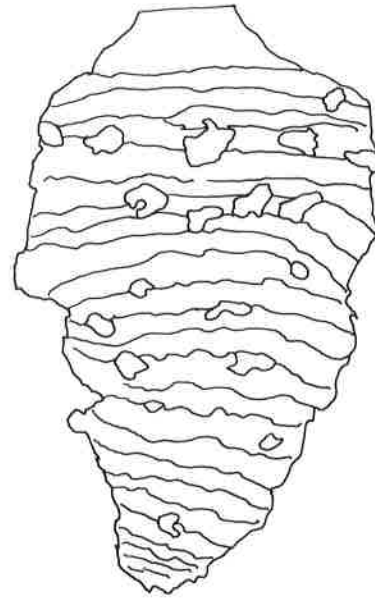


Fig. 2. Drawing of a rootstock of *T. erectum*, traced from a photograph, showing the annual constrictions

Table 1. Frequencies of *Trillium* plants with 1, 2, 3, 4, and 5 flowers obtained in a census of the study plot during 1978

	1 fl.	2 fl.	3 fl.	4 fl.	5 fl.	Total
Number of plants	600	91	10	5	1	707
Number of flowers	600	182	30	20	5	837

1 flower. Most multiflowered plants were double flowered (91), although rarely plants with 3, 4, or 5 flowers were encountered (Table 1).

Plant Survivorship and Changes in Flowering State

Of the original 128 tagged plants, 124 were present the following spring, indicating very high survivorship (96.9%). It must be emphasized that only mature plants were included in the tagging experiment. Species of the genus *Trillium* usually require a minimum of 7 years from the time of germination to produce the first flower (Patrick 1973). The survivorship of young seedlings may be much lower than the figure obtained for mature plants.

The results of the tagging experiment (Table 2) show that while most plants produce the same number of flowers from one year to the next, some plants do change their flowering state. Excluding the few missing plants, no previously flowered plant was observed in a nonflowering state.

Flower Predation

In 1977 and 1978, more than 20% of all flowers were destroyed by the *Clepsia* larvae, but in 1980 less than 5% were infested (Table 3). The likelihood that a plant would be infested varied significantly depending upon whether 1 flower, 2 flowers, or 3 or more flowers were produced ($X^2=28.57$, $p<0.001$, variance test for homogeneity of the binomial distribution, Snedecor and Cochran 1973, Table 3, 1978 data). However, the actual flower infestation rate was the same in all 3 groups ($X^2=0.702$, $p>0.5$,

Table 2. Survivorship and flowering state of tagged *Trillium* plants. Numbers in parentheses indicate number of plants originally tagged in 1979. Numbers in the chart represent the flowering state one year later

	0 flower	1 flower	2 flowers	Disappeared
Nonflowering plants (N=4)	3	1	0	0
Single flowering plants (N=111)	0	105	3	3
Double flowering plants (N=13)	0	7	5	1

Table 3. Flower predation summary for 1977, 1978, and 1980. Numbers in parentheses indicate sample sizes

	1977	1978	1980
Frequency of flower infestation			
Single flowered plants	—	20.2% (600)	4.2% (140)
Double flowered plants	—	22.5% (182)	5.0% (60)
Plants with 3 or more flowers	—	23.6% (55)	—
Total, all flowers	23.6% (196)	20.9% (837)	4.5% (200)
Frequency of plant infestation			
Single flowered plants	—	20.2% (600)	4.2% (140)
Double flowered plants	—	38.5% (91)	10.0% (30)
Plants with 3 or more flowers	—	62.5% (16)	—
Frequency of total reproductive failure (all flowers on a plant infested)			
Single flowered plants	—	20.2% (600)	4.2% (140)
Double flowered plants	—	6.6% (91)	0% (30)
Plants with 3 or more flowers	—	0% (16)	—

Table 3). That is, the probability of infestation for a given flower was the same whether the flower was from a single or multiflowered plant. The implication of the common flower infestation rate is that single flowered plants were significantly more likely to have their entire annual reproductive effort destroyed by the *Clepsis* larvae than were the multiflowered plants ($X^2=13.51$, $p<0.005$, Table 3).

Insect Visitation

While the flower predation rate was the same for both types of plants, flowers from double flowered plants attracted 50% more pollinators than those from single flowered plants. Flowers from single flowered plants that had been covered with Tangle-foot ($N=52$) trapped 3.7 ± 3.2 flies during the 4 day test period compared with 5.6 ± 4.4 flies by flowers from double flowered plants ($N=42$). There was considerable flower to flower variation. One flower contained 24 trapped insects, and a few contained none. However, the difference between the visitation rates of the two types of plants is significant ($p<0.02$; Wilcoxon two sample test).

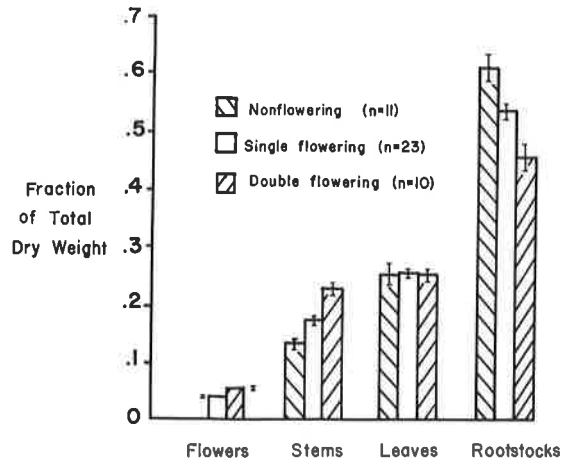


Fig. 3. Fraction of total dry weight of various plant parts for nonflowering, single flowering, and double flowering plants. The three groups are significantly different with respect to the proportion of biomass allotted to flowers, stems, and rootstocks ($p<0.01$) but not leaves ($p>0.5$) (Kruskal Wallis test). Standard error bars are shown

Table 4. Frequencies of single and multiflowered displays for small (1.5 g or less) and large (greater than 1.5 g) rootstocks. $X^2=7.23$, $p<0.01$

	1 flower	2 or more flowers
Rootstock		
1.5 g or less	18	3
Greater than 1.5 g	5	9

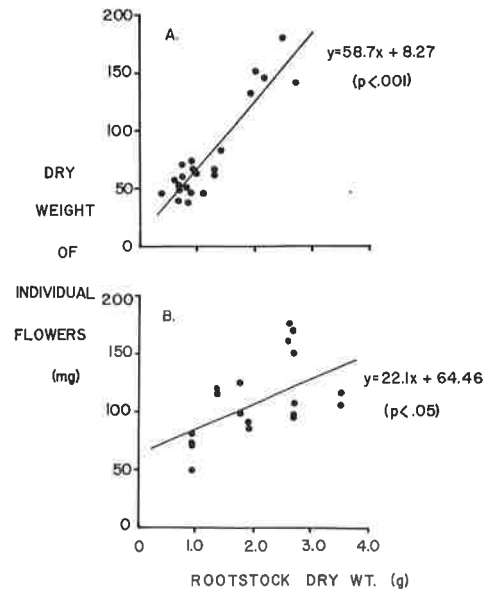


Fig. 4. Dry weight of individual flowers shown as a function of rootstock dry weight for single flowering (A) and double flowering (B) plants

Energy Allocation

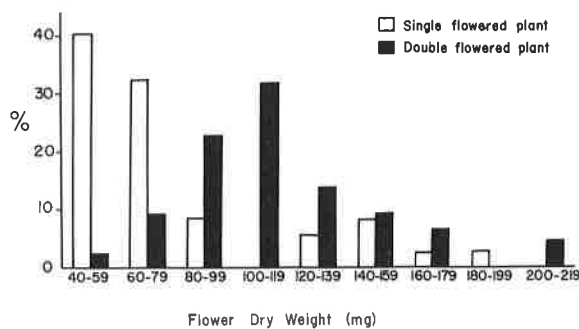
The fraction of the total dry weight represented by the various plant parts is quite uniform within each of the 3 groups (nonflowering, single flowering, and double flowering plants), but significant variation occurs between groups (Fig. 3). Single and double

Table 5. Mean dry weight (g) of different plant tissue from nonflowering, single flowering and double flowering *Trillium* plants. Standard deviations are shown

	Flowers	Sterns	Leaves	Rootstock	Total plant
Nonflowering plants ($N=11$)	—	0.100 ± 0.057	0.181 ± 0.084	0.501 ± 0.341	0.781 ± 0.467
Single flowering plants ($N=23$)	0.078 ± 0.041	0.361 ± 0.206	0.538 ± 0.310	1.177 ± 0.650	2.152 ± 1.155
Double flowering plants ($N=10$)	0.224 ± 0.071	0.955 ± 0.275	1.059 ± 0.418	2.100 ± 0.870	4.388 ± 1.444

flowered plants differed in the proportion of above ground biomass (dry weight) allocated to flowers (8.7% vs 11.1%, $t=2.83$, $p<0.01$; data was arcsine transformed for analysis). There was found to be significant uniformity in the size of the two shoots (stems, leaves, and flowers) produced by a double flowered plant ($r=0.942$, $p<0.001$, intraclass correlation coefficient, Zar 1974).

The number of flowers produced by a plant is associated with the size of its rootstock. That is, big rootstocks are more likely to produce 2 flowers than are small rootstocks (Table 4).

**Fig. 5.** Distribution of dry weights of individual flowers from single ($n=37$) and double flowered ($n=44$) plants**Table 6.** Number of annual constrictions and width of internodes for nonflowering, single flowering, and double flowering plants. Standard deviations are shown

	Non flowering plants ($N=11$)	Single flowering plants ($N=23$)	Double flowering plants ($N=10$)
Mean number of annual constrictions	14.5 ± 4.9	20.3 ± 4.9	21.2 ± 3.0
Range in the number of annual constrictions	5–23	11–29	16–26
Mean width of internodes (mm)	1.29 ± 0.34	1.25 ± 0.29	1.59 ± 0.22

Table 7. Fecundity of single flowered plants during 1978, 1979, and 1980 and of double flowered plants during 1980. Numbers in parentheses indicate number of flowers examined. Standard deviations are shown

	Number of ovules produced per flower			Number of seeds produced per flower			Rate of seed set		
	1978	1979	1980	1978	1979	1980	1978	1979	1980
Single flowering plants	26.0 ± 9.8 (13)	16.0 ± 7.2 (9)	23.3 ± 9.0 (27)	13.9 ± 8.8 (13)	9.6 ± 5.2 (9)	15.2 ± 6.1 (27)	53.5% (613)	60.0% (9)	65.2% (27)
Double flowering plants	—	—	39.9 ± 12.6 (30)	—	—	21.6 ± 8.5 (30)	—	—	54.1% (30)

Not only the number of flowers, but the size of the flowers increases as the size of the rootstock increases (Fig. 4).

While the absolute reproductive effort is greater in double flowered plants (Table 5), this is not simply because an additional flower is produced. The flowers produced by double flowered plants are also significantly larger ($p<0.01$, Wilcoxon two sample test; Fig. 5).

Overall, double flowered plants are significantly larger (total dry weight) than single flowered plants ($t=4.72$, $p<0.001$). Significantly the rootstocks of single and double flowered plants do not differ in the number of annual constrictions ($t=0.54$, $p>0.5$; Table 6), however the internodes from double flowered plants are significantly wider than those from single flowered plants ($t=3.29$, $p<0.005$; Table 6), indicating greater annual growth among double flowered plants.

Seed Set

All flowers examined in this study ($n=79$) produced seeds (Table 7). The proportion of ovules fertilized ranged from 25% to 100% in single flowered plants, and from 30% to 83% in double flowered plants. A strong correlation exists between the dry weight of a flower and the number of ovules produced ($r=0.89$, $p<0.001$, Fig. 6). Moreover, a strong correlation exists between the number of ovules produced, and the number that are fertilized ($r=0.82$, $p<0.001$, Fig. 7).

In summary then, as the rootstock increases in size, it produces larger flowers which produce more ovules which yield more seeds. At the same time, an increase in the size of the rootstock may result in an additional flower, which reduces the impact of the flower predation by the Tortricid larvae and may increase visitation rates by dipterans. These relationships are summarized in Fig. 8.

Annual Fitness of Single and Double Flowered Plants

Using the data obtained in this study, it is possible to estimate the annual fitness of double flowered plants relative to single flowered plants. The relative fitness of double flowered plants (W_d) is equal to the number of seeds produced by double flowered plants (S_d) divided by the number of seeds produced by

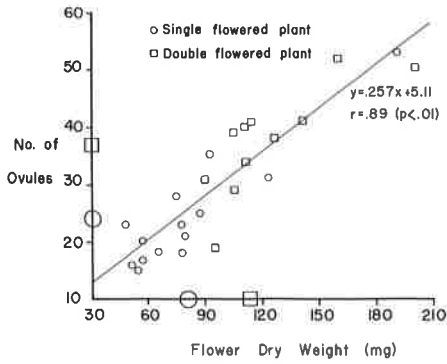


Fig. 6. Number of ovules produced shown as a function of flower dry weight. Ovules represent those counted in only one of the three ovary locules. Therefore, the total number of ovules produced is approximately three times the number shown. The mean values for the dependent and independent variables are indicated on the respective axes

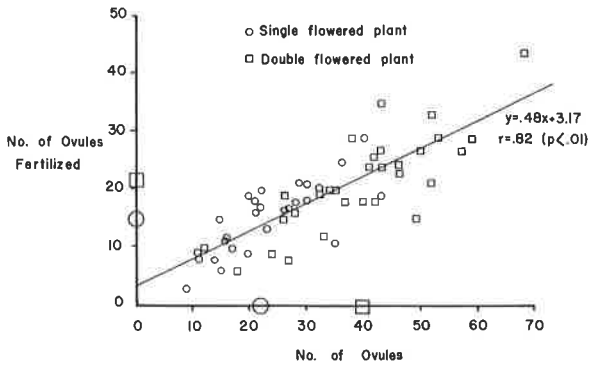


Fig. 7. Absolute seed set shown as a function of number of ovules produced. The mean values for the dependent and independent variables are indicated on the respective axes

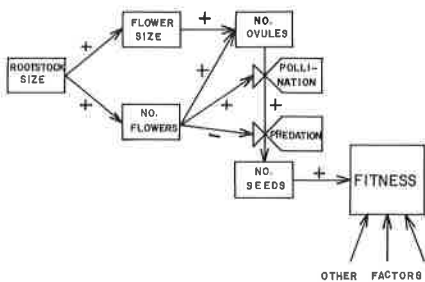


Fig. 8. A flow diagram showing the effect of rootstock size on seed set via the size and number of flowers produced. A plus sign denotes a positive correlation between 2 factors, a minus sign denotes a negative correlation

single flowered plants (S_s). S_d and S_s can be determined from the following equations:

$$S_d = F_d \times O_d \times T_d \times P_d$$

$$S_s = F_s \times O_s \times T_s \times P_s$$

where

S = Number of seeds produced;

F = Mean number of flowers per plant;

O = Mean number of ovules per flower;

T = Probability an ovule will be fertilized;

P = Probability a seed will escape predation.

W_d , that is S_d/S_s , can be calculated by substituting the observed values into the equations.

$$F_d = 2.0$$

$$F_s = 1.0$$

$$O_d = 119.7 \text{ (i.e., } 3 \times 39.9 \text{; 1980 data)}$$

$$O_s = 69.9 \text{ (i.e., } 3 \times 23.3 \text{; 1980 data)}$$

$$T_d = 0.541 \text{ (1980 data)}$$

$$T_s = 0.652 \text{ (1980 data)}$$

$$P_d = 0.775 \text{ (1978 data)}$$

$$P_s = 0.798 \text{ (1978 data)}$$

Therefore, $W_d = 2.76$.

Double flowered plants seem to be far more fit than single flowered plants. Yet single flowered plants are 6 to 7 times more common in the population.

Discussion

If the predation of 2 or more flowers on the same plant consists of independent events, that is if no resource concentration effect (Root 1973) is shown, then the expected frequency of plants with varying degrees of infestation can be calculated directly from the overall infestation rate. Tables 8 and 9 show that the observed and predicted frequencies are almost identical. The reason no concentration effect was exhibited is probably due to the fact that the resource concentration hypothesis was conceived with adult flying insects in mind, particularly Chrysomelid beetles and *Pieris* butterflies (Root 1973), insects which possess both well developed locomotor and sensory abilities. In this study, the Tortricid larvae, once on the ground, are first not particularly mobile, and second not in a position to survey the landscape for *Trillium* plants. I suspect they are responsive to *Trillium* stems, which they crawl up, and not to the floral display.

The pollinators, on the other hand, do seem to be attracted to the larger floral displays of the multiflowered plants, a finding which agrees with other studies (Mulligan and Kevan 1973; Willson and Price 1978). Janzen (1967) suggested that certain tropical trees attract pollinators by opening all their flowers simultaneously, thereby standing out conspicuously against the forest background. It is possible that on a much smaller scale, multiflowered plants achieve similar visibility when perceived against the background of the forest floor. Or insect visitors

Table 8. Predicted and observed values for 0, 1, and 2 infested (I) flowers in double flowered plants. 1978 data. Predictions were made using the general flower infestation rate (20.9%) and assuming independence. See text

	I=0	I=1	I=2
Predicted	56.94	30.09	3.97
Observed	56	29	6

Table 9. Predicted and observed values for complete reproductive failure (all flowers eaten) in plants with 1, 2, 3, 4, and 5 flowers. 1978 data. Predictions made as in Table 8

	1	2	3	4	5
Predicted	125.4	3.97	0.09	0.01	0.0004
Observed	121	6	0	0	0

could be attracted to the stronger odor emitted by double flowered plants, which may be due to the larger size of the flowers, as well as the increased number of flowers. It is also possible that the variation in visitation rates is due to other factors such as the amount of sunlight received by a plant, a factor that was not controlled in this study.

Although in a given year, multiflowered individuals are reproductively superior to single flowered plants, this advantage might be negated if multiflowered plants exhibit lower survivorship than single flowered individuals (Williams 1966). Schemske (1980) postulated that low survivorship among all plants also might favor the production of small suboptimal floral displays by selecting against reproductive delays, which could be used by the plant to amass energy to produce more than a single flower. The tagging experiment provides no evidence of this, however. *T. erectum* is a slow growing, long lived perennial herb of mature forests. (The rootstock of one of the triple flowered plants exhibited 32 annual constrictions). It appears that once established, *T. erectum* enjoys high survivorship in all flowering states.

It is possible that multifloweredness involves a maturation process, and that all, or at least most plants eventually produce a second flower. However, rootstocks from single and multiflowered plants do not differ in the number of annual constrictions (Table 5). It must be pointed out that the oldest portion of the rootstock sometimes rots away (Brandt 1916), meaning that the age of the plant may be underestimated by counting the annual constrictions. It is possible that, given the soil and drainage conditions in the study plot, annual constrictions persist for 20–30 years and then that section of the rootstock rots away. Thus, if one plant were older than another, but both were older than 30 years, it would be impossible to determine the older individual. In other words, while there is no evidence that double flowered plants are older than single flowered plants, the possibility cannot be ruled out. What is clear is that double flowered plants exhibit more annual growth than single flowered plants (Table 6). This finding strongly supports the idea that the size of the floral display is governed by available resources.

In *Trillium spp.*, stem buds are produced by the rootstock 1 or even 2 years before they appear above ground (Brandt 1916). In a study of *T. sessile* and *T. ovatum*, Brandt (1916) discovered a critical period for the stem buds, which in California occurs late in May. Those buds with promordia well advanced proceed to develop and produce new shoots the following year. Others, with tissue less differentiated have their development suspended. Some of these suspended buds resume development the following year, however, for those which have already begun the develop primordia, the suspension is usually fatal (Brandt 1916). Brandt showed that this selective elimination of stem buds is guided by the amount of energy available to the plant, such that the number of stem buds which pass the critical period sometimes varies from year to year. He found that while only 1 of the 2 stem buds usually produced annually by *T. ovatum* develop into a stem under most conditions, both buds will develop if the plant is given an unusual amount of light. He also observed that in partially cleared forested areas, *T. ovatum* regularly sends up 2 shoots.

The paradox arising from previous studies was that the most successful floral displays were the least common displays. This study shows that, in *Trillium* at least, the size of the floral display (the number and size of the flowers) is correlated with the size of the energy reserves, i.e., the size of the rootstock. Thus, instead of framing the paradox in terms of the floral display, one could frame it in terms of the rootstocks. The problem then becomes:

plants with large rootstocks produce the most seeds, yet plants with large rootstocks are rare in the population. When stated this way, the paradox disappears. The size of the rootstock is not the result of evolutionary pressures, but is a function of the plant's age and the available energy.

There is a problem in applying the optimality approach to plants, which is that plants exhibit indeterminate growth. For the most part, given enough nutrients and time, plants will continue to grow larger and larger. Since there is no definite adult size, and since the sizes of many traits are primarily a function of plants size, the existence of an optimal size for these traits is questionable.

Studies of a number of herbaceous species have shown that an increase in plant size results in an increase in fecundity (Werner 1975; Willson et al. 1979; Solbrig et al. 1980; Zimmerman 1980). In addition, other benefits may accrue to larger plants, such as increased survivorship (Cook 1979; Solbrig et al. 1980). It appears that it is to a plant's advantage to grow as large as it can and to produce as many flowers and as large a floral display as it can afford. Big old plants, which are probably in the minority in most populations, can afford more than little young ones, which explains why the most successful floral displays are usually the least common.

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