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An Experimental Study of Floral Display and Fruit Set in *Chilopsis linearis* (Bignoniaceae)

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Summary. To examine the effects of pollen and resource availability on floral display and fruit set in *Chilopsis linearis* three different types of experimental manipulations were performed. Pollen availability to individual inflorescences was altered by combinations of hand-pollinations and/or pollinator exclusions. Number of flowers produced per inflorescence was determinate; it was not affected by pollination, although flowers of the unpollinated treatment lasted longer. Fruit set was increased over natural levels by an average of 540% by hand-pollinating individual inflorescences. There was also a negative correlation between inflorescence size and percent fruit set in all treatments tested. Attempts to vary resources available to individual inflorescences and entire trees showed no significant effect on fruit set. These results show that, at the level of individual inflorescences, fruit and seed production in *Chilopsis linearis* are pollen limited and not resource limited. The problem of testing for resource limitation of female reproductive success in iteroparous plants and the effect of inflorescence size on female components of fitness are also discussed.

Introduction

In order to better understand plant breeding systems and plant-pollinator coevolution, additional information on the relationships between floral display, pollinator activity, and seed set is required. In hermaphroditic plants with perfect flowers, reproductive success is dependent not only on seed dispersal and germination, but also on the two sexual functions: male function, production and dissemination of pollen; and female function, production of ovules and maturation of fruits and seeds. The allocation of resources between these functions and the extent to which each may limit reproductive success recently have been the subject of both theoretical and empirical investigation, but little consensus has yet emerged (Charnov 1979; Stephenson 1979, 1980; Udovic and Aker ms. Sutherland ms). Many reproductive structures in plants, such as those involved in floral display, serve both male and female functions. To understand the evolution of breeding systems it is necessary to know the extent to which availability of pollen and resources affect reproductive success. Much can be learned from controlled manipulative experiments on plants growing under natural

conditions (e.g., Waser 1978; Stephenson 1979, 1980; Sutherland ms).

In the present paper we describe results of a series of experiments designed to test for effects of pollen and resource limitation on seed and fruit set of desert willow, *Chilopsis linearis* Sweet. We performed three kinds of experiments. First, we manipulated the availability of pollen by combinations of bagging and hand-pollinating all flowers on particular inflorescences. Second, we reduced the numbers of buds and adjacent leaves on inflorescences in separate experiments in order to evaluate the possibility of local resource limitation. Finally, we manipulated the availability of water to individual trees. We measured the effects of these experimental manipulations on the production and longevity of flowers and on fruit and seed set.

Chilopsis linearis provides a good system for such a study. It is a long-lived tree which grows abundantly along intermittent desert watercourses. In late spring and early summer it produces numerous showy zygomorphic flowers on terminal inflorescences. Although a variety of animals are attracted to their nectar, these flowers appear to be specialized for pollination by large bees of the genera *Bombus* and *Xylocopa* (Whittam 1977; Brown et al. 1981). The large robust flowers and flexible branches facilitate manipulation of inflorescences with minimal damage, and the large pods which retain their seeds make it easy to quantify female reproductive success.

Materials and Methods

Study Site

The present study was conducted along the Cañada del Oro Wash, elevation 910 m, near the western base of the Santa Catalina Mountains 23 km north of Tucson, Arizona. Dominant vegetation includes mesquite (*Prosopis velutina*) and catclaw acacia (*Acacia gregii*) in surrounding habitat with desert willow, Arizona walnut (*Juglans major*), and Arizona ash (*Fraxinus velutina*) restricted to the wash. Ten desert willow trees varying in height from 3 to 10 m and growing within 200 m of one another were used in the experiments. The study was conducted from May through September, 1979.

Experimental Design

The ten trees were paired according to size, flower abundance, and location along the wash. One tree in each pair

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was randomly designated to be watered and it received extra water sufficient to saturate the soil approximately twice weekly from late June to the end of August. The other tree in the pair was left alone and served as a control to test for effects of water on reproductive success.

Individual inflorescences within a tree were assigned to one of five experimental treatments: 1. bagged with fine meshed nylon to exclude all pollinators and nectar feeders; 2. bagged (as above) and hand-pollinated daily; 3. unbagged and hand-pollinated daily; 4. unbagged and approximately one-half of the buds removed as they matured; 5. unbagged, unmanipulated control. Experimental inflorescences were marked individually with coded tags. Pollen for all hand pollination treatments was collected from fresh flowers obtained from bagged inflorescences on three donor trees which were used on alternate days (two one day, one the next). The donor trees were not used in any of the experimental manipulations. Pollen was collected from dehiscid anthers and applied to stigmas using a small (# 1 or # 2) brush. Open flowers of the hand-pollination treatments were hand-pollinated daily between 0800 and 1100 h from May 24 to June 28, 1979. These dates encompassed the entire flowering period of the experimental inflorescences, and the peak flowering of the trees, although a few other inflorescences on the same trees began flowering before and continued to flower after the experiments were terminated. Each experimental treatment was replicated 5 times on each tree. We used a block design so that each replicate consisted of 5 inflorescences of similar size and location on the tree.

An additional experiment to test for the effect of local resource limitation was performed by pairing similar inflorescences that had not yet begun flowering, removing half of the leaves on the branch adjacent to one inflorescence, and leaving the other inflorescence as an unmanipulated control. These treatments were replicated five times on each tree.

Data Collection

The number of flowers open per inflorescence was recorded daily from May 24 to June 28, 1979. After the fruits had matured, on September 2, 1979, all inflorescences were collected and dried. The total number of flowers per inflorescence was determined by counting flower scars. For each inflorescence we also recorded number of fruits, and number and weight of seeds per fruit.

Results

Floral Display

The daily pattern of floral display for all control inflorescences on 3 trees is illustrated in Fig. 1. Although this represents a very small fraction of the total flowers on these trees, it reflects the even distribution of daily flower production by trees throughout most of the flowering period. Production of flowers on the five individual control inflorescences of one tree are shown separately in Fig. 2. Despite impressions of temporal clumping within an inflorescence, flowers were produced randomly over the flowering season. Out of 50 inflorescences monitored, 40 were random, 9 even, and 1 clumped (Chi-square comparison with a Poisson distribution, Pielou 1969).

Although there was no significant difference in total number of flowers produced per inflorescence between

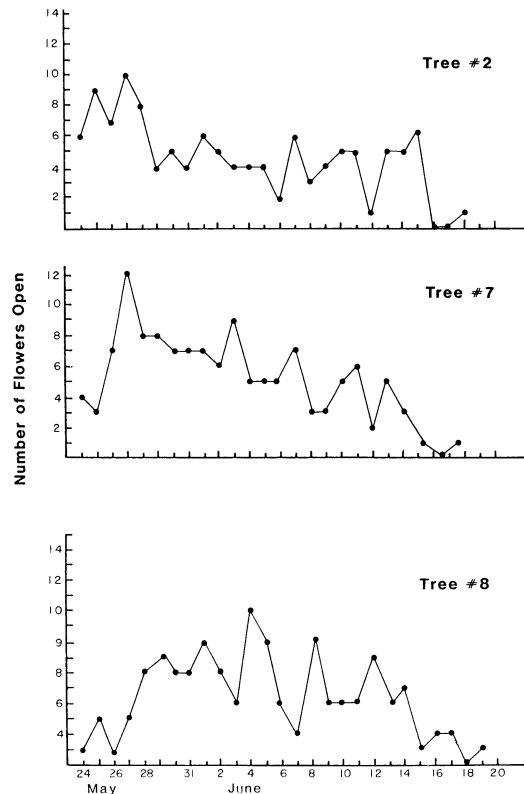


Fig. 1. Total number of flowers open per day on all control inflorescences on three trees. Dates encompass the total flowering period of control inflorescences

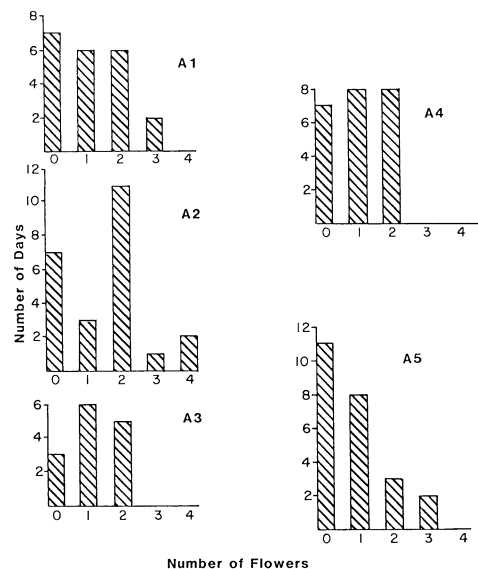


Fig. 2. Frequency distribution of the number of flowers open per day for the five control inflorescences of tree # 2. The data include the entire flowering period of each inflorescence under study

treatments (ANOVA, $P > 0.05$), flowers on the bagged inflorescences lasted longer than those of the other treatments (average flower life: bagged 2.28 days, bagged and hand pollinated 1.52 days, control 1.38 days, unbagged and hand pollinated 1.37 days, $P < 0.01$, Student-Newman-Kuels test). There was a highly significant difference between ex-

Table 1. A. Analysis of variance of fruit set for manipulation of pollination and resource availability. B. Results of a Student-Newman-Kuels test to determine levels of significance between individual treatments. All data are expressed in terms of number of fruits per inflorescence

		df	SS	MS	F	P
A.	Blocks	16	5.4	0.34		
	Watering	1	0.04	0.04	0.57	0.25 < < 0.5
	Error	16	1.06	0.07		
	Inflorescence treatments	3	45.38	15.13	126.08	< 0.001
	Interaction (Inflorescence × water)	3	2.87	0.96	8.00	< 0.001
	Error	96	11.45	0.12		
B.*	bagged and hand pollinated (5.79)	> unbagged and hand pollinated (3.97)	> unmanipulated control (1.07)	> half buds removed (0.72)	> bagged (0.12)	

* All differences significant at $P < 0.05$ using a two-tailed test except unmanipulated control and half buds removed which is significant at $P < 0.05$ using a one-tailed test

perimental blocks ($P < 0.001$) which is not surprising, since blocks were chosen in part on the basis of size of inflorescences. These results show that the number of flowers produced per inflorescence is determinate and not influenced by pollination success.

Fruit and Seed Set

The patterns of both fruit and seed set varied among treatments in a similar fashion. We present data for fruit set rather than seed set, because the former data could be normalized and then tested using parametric statistics.

Pollination Treatments

There were highly significant differences in the effects of the various pollination treatments on fruit set (ANOVA, $P < 0.001$, Table 1). In order to identify the magnitude of various treatment effects a Student-Newman-Kuels test was performed. The treatments ranked as follows in order of decreasing number of fruits per inflorescence: bagged and hand pollinated > unbagged and hand pollinated > unmanipulated control > half buds removed > bagged (Table 1). These results show that the availability of pollen limits fruit set on individual inflorescences in *Chilopsis linearis*. Application of outcrossed pollen increased fruit set above natural levels especially when flowers had been bagged to exclude pollinators. Inflorescences bagged and not pollinated produced virtually no fruits suggesting that *C. linearis* is self-incompatible.

Resource Treatments

None of the experimental manipulations suggest that fruit set of individual inflorescences was limited by available resources. If local availability of resources limits fruit set, we expect higher fruit set per flower after one-half of the buds had been removed, because approximately twice as many resources per flower would be available to mature fruits. Although 54.3% of the flowers were removed, the number of fruits per inflorescence also was reduced by approximately one-half (Table 1), so that the number of fruits per flower did not differ significantly between the treatment and the control (t -test, $P > 0.2$).

In a second test for local resource limitation we removed one-half of the leaves on the branch in the expectation that this might reduce fruit set. Number of fruits on treated inflorescences did not differ from controls ($P > 0.25$, Wilcoxon matched-pair signed ranks test).

In an attempt to manipulate resource availability at the level of entire trees, one-half of the trees were watered. We expected water to be the primary resource limiting productivity of *C. linearis* during the summer growing season. However, watering had no effect on fruit set (Table 1, $P > 0.25$).

Discussion

Floral Display

Floral display in *Chilopsis linearis* appears to follow the "cornucopia" strategy that is typical of temperate Bignoniaceae (Gentry 1974). A large number of flowers are produced continuously over several weeks. Although individual inflorescences appear to have high initial flowering rates, the pattern for an entire tree, with the onset of flowering by inflorescences staggered over the first few weeks of the season, will more closely approximate a normal curve. One of the criteria in choosing inflorescences used in the experiments was that the inflorescences had not begun flowering before May 24.

To investigate the relationship between inflorescence size and female function, inflorescence size was regressed against number of fruits and percent fruit set (Table 2). For the three experimental treatments tested, only the hand pollinated and bagged treatment showed a positive correlation between number of fruit set and inflorescence size. Both treatments that were exposed to natural pollination did not show a significant effect. All treatments showed a significant decrease in percent fruit set with inflorescence size. On a per flower basis, larger inflorescences devote less to female function. Because larger *C. linearis* trees tend to have larger inflorescences (pers. obs.), this relationship suggests that allocation to male and female function may also change with tree size. This relationship between individual size, allocation of resources to each sex, and reproductive success through male and female function needs to be examined more closely.

Table 2. Correlation coefficients and regression equations for inflorescence size and number of fruits or percent seed set. r = linear correlation coefficient, x = inflorescence size, y = number of fruits or percent fruit set, n = sample size, ns = not significant

	Control	Hand pollinated and unbagged	Hand pollinated and bagged
Number of fruits	ns $n=43$	ns $n=41$	$r=0.36^*$ $y=0.16x+2.79$ $n=41$
Percent fruit set	$r=0.37^*$ $y=-0.003x+0.12$ $n=43$ * $P<0.05$ ** $P<0.01$	$r=0.47^{**}$ $y=-0.007x+0.36$ $n=41$	$r=0.39^{**}$ $y=-0.01x+0.51$ $n=41$

Fruit and Seed Set

Inflorescences that were bagged and not hand-pollinated set virtually no fruits. The four pods that matured in this treatment could be traced to instances of accidental removal of bags for a single day. Additional experiments by L. Delph and A. Kodric-Brown showed that bagged inflorescences did not set fruit when pollen from other flowers on the same tree was used. These results show that *C. linearis* is self incompatible. Unpollinated flowers lasted longer than those which had been pollinated. Apparently this represents an adaptive response to increase pollination success in an obligately outcrossed plant which produces a determinate number of flowers.

Availability of outcrossed pollen limited fruit set on individual inflorescences. This is demonstrated by the fact that hand-pollinated inflorescences had higher fruit set than naturally pollinated ones (Table 1). An interesting finding was that inflorescences bagged before and after hand-pollination had higher fruit set than those which were also hand-pollinated but were left unbagged and exposed to visits by natural pollinators. We can think of two explanations for these results. First, stigmatic surfaces may be so occluded by selfed pollen as to prevent deposition of sufficient outcrossed pollen to achieve maximal fruit set. This is likely because the insects visiting the flowers tend to visit sequentially many flowers on the same tree. Second, many of the inflorescences may have been visited recently by natural pollinators and consequently had closed stigmas which would not have been receptive to the pollen we attempted to apply. *C. linearis* has thigmotactic stigmas which close within a few seconds of contact. Regardless of the mechanism responsible, these results may be somewhat anomalous because the flowers were being visited primarily by *Apis mellifera*. This European honey bee is not native to the study site and may be a relatively ineffective pollinator of *Chilopsis*, which is coevolved for pollination by larger native bees (Whittam 1977; Brown et al. 1981). From the hand-pollination experiments we conclude that fruit set on individual inflorescences in this population is limited by insufficient quantities of outcrossed pollen and probably by inadequate movement of pollinators between individual trees.

Despite our initial expectations, both experiments to test for limitation of local resources showed no effect on fruit set. We attempted to increase the availability of resources to individual fruits by removing one-half of the flower buds, and to reduce resources by removing one-half of the adjacent leaves. In both cases the number of fruits set per flower

did not differ from the controls. We conclude that local levels of resources such as carbohydrates, minerals, or water do not limit fruit set.

The results presented so far do not rule out the possibility that resources are limiting at the level of individual trees but are freely translocated within a tree so they do not appreciably limit fruit set at the level of individual inflorescences. We attempted to test this possibility by supplying the one resource, water, which seemed to be most likely to limit primary production and fruit set in *Chilopsis*. However, watering of individual trees had no effect on fruit set (Table 1). There may be two reasons this experiment is inadequate to test the hypothesis of resource limitation. First, water may not have been a limiting resource, especially in the year we conducted our experiments. Our study area received more rainfall in the seven months prior to our experiments than in the same period in any of the previous twenty years (rainfall data from Oracle, Arizona, 15 miles upstream of the study site). Because the soil was still saturated, we did not begin watering until early June when many fruits had already begun to mature. Second, in perennials such as *Chilopsis* with terminal inflorescences and determinate flower buds, allocation to reproduction may be determined by resources available from stores accumulated during the previous growing season rather than by resources acquired during the current season. However, we do not believe watering in the previous season would have been a better test of resource limitation. Had we watered prior to the flowering period, the plants could have responded by increasing the number of inflorescences. Once the number of inflorescences was determined by the plants, additional water was available for the plant to allocate to individual inflorescences or vegetative growth.

Recent theoretical considerations of plant breeding systems and reproductive strategies have emphasized the potentially different selective pressures and constraints on male and female function (Charnov 1979; see also Janzen 1977; Willson 1979; Kodric-Brown and Brown 1979). Charnov suggested that if Bateman's principle (1948) applies to hermaphroditic plants then female function (seed set) should be limited by available resources whereas male function (fertilization of ovules) should be limited by competition for access to receptive ovules and hence by availability of pollinators. If true, this idea implies that the majority of plant-pollinator coevolution occurs through male function. Empirical evidence suggests that Bateman's principle may apply to some but not all hermaphroditic plants. Detailed studies of monocarpic species such as *Yucca whip-*

plei and *Agave* spp. indicate that seed set and fruit production is limited primarily by resources (Udovich and Aker ms, Sutherland ms). On the other hand, several studies provide evidence for pollinator limitation of female function in iteroparous perennials (e.g., Waser 1978; Schemske 1980; Zimmerman 1980). However, even closely related species of perennials may differ in the extent to which female function is pollen limited. Stephenson (1979, 1980), in an experimental study of *Catalpa speciosa* (which is in the same family, Bignoniaceae, as *Chilopsis*) showed that the number of fruits per inflorescence was relatively fixed and largely independent of pollination success, but it was limited by local availability of resources as demonstrated by reduction in fruit set following removal of leaves adjacent to inflorescences. Since these findings obviously differ from our results for *Chilopsis*, it is apparent that more empirical work must be done to understand the general processes which affect the evolution of reproductive and pollination strategies in higher plants. In perennials the situation is complicated by the fact that resource and pollination limitation cannot be easily separated, because plants can potentially allocate resources differentially to growth or current reproduction depending on immediate pollination success. Thus, for example, while pollination success clearly limits fruit set of *Chilopsis linearis* at the level of individual inflorescences, experimental manipulations of resource levels over several growing seasons and of pollen availability for entire plants are necessary to determine the extent to which resource availability may also affect female function.

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References

Bateman AJ (1948) Intra-sexual selection in *Drosophila*. *Heredity* 2: 349–368

- Brown JH, Kodric-Brown A, Whitham TG, Bond HW (1981) Competition between hummingbirds and insects for the nectar of two species of shrubs. *Southwestern Naturalist* 26:133–145
- Charnov EL (1979) Simultaneous hermaphroditism and sexual selection. *Proc Nat Acad Sci U.S.* 76:2480–2484
- Gentry AH (1974) Coevolutionary patterns in Central American Bignoniaceae. *Ann Miss Bot Gard* 61:728–759
- Janzen DH (1977) A note on optimal mate selection by plants. *American Naturalist* 111:365–371
- Kodric-Brown A, Brown JH (1979) Competition between distantly related taxa in the coevolution of plants and pollinators. *American Zoologist* 19:1115–1127
- Pielou EC (1969) An introduction to mathematical ecology. New York: Wiley-Interscience, John Wiley and Sons, Inc
- Schemske DW (1980) Evolution of floral display in the orchid *Brassavola nodosa*. *Evolution* 34:489–493
- Stephenson AG (1979) An evolutionary examination of the floral display of *Catalpa speciosa* (Bignoniaceae). *Evolution* 33:1200–1209
- Stephenson AG (1980) Fruit set, herbivory, fruit reduction, and the fruiting strategy of *Catalpa speciosa* (Bignoniaceae). *Ecology* 61:57–64
- Sutherland S (Manuscript) Resource-limited fruit set in paniculate agaves: a test of Bateman's principle
- Udovich D, Aker C (in press) Fruit abortion and the regulation of fruit number in *Yucca whipplei* *Oecologia*
- Waser NM (1978) Competition for hummingbird pollination and sequential flowering in two Colorado wildflowers. *Ecology* 59:934–944
- Whitham TG Coevolution of foraging in *Bombus* and nectar dispensing in *Chilopsis*: A last dreg theory. *Science* 197:593–596
- Willson MF (1979) Sexual selection in plants. *American Naturalist* 113:777–790
- Zimmerman M (1980) Reproduction in *Polemonium*: competition for pollinators. *Ecology* 61:497–501

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