

Determinants of Fruit Set in *Yucca whipplei*: Reproductive Expenditure vs. Pollinator Availability

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Summary. The number of flowers produced by inflorescences of *Yucca whipplei* (Agavaceae) consistently exceeds the number of fruits produced by about one order of magnitude. To determine the factors responsible for low fruit set, the relation between pollinator availability, the amount of resources spent on reproduction (as indicated by inflorescence size), and the number of fruits matured was studied during 1978 and 1979 at 18 locations in chaparral, coastal sage scrub, and desert scrub communities of southern California.

The following results support the conclusion that pollinators do not usually limit fruit production in *Yucca whipplei*. Rather, fruit production is limited by the amount of resources available to support developing fruits. (1) Fruit production is positively correlated with inflorescence size both within and between populations. The average size of inflorescence for a population is an excellent predictor of mean fruit production. Furthermore, 54% of the total variance in fruit production of individual plants can be explained by inflorescence size. (2) In contrast, although fruit production within most populations is positively correlated with an index of the number of pollinator visits to an inflorescence, the relative abundance of pollinators for a population is a poor predictor of mean fruit production, and only 9% of the total variance in fruit production can be explained by the visitation index. Furthermore, at four sites studied for two years, there was little change in average inflorescence size or fruit production from 1978 to 1979, despite large differences in relative abundance of pollinators at each of the sites. (3) Based on geographic proximity, and physiographic and vegetational similarities, study sites were grouped into regional clusters. Both inflorescence size and fruit production varied considerably between regions. Of the total variation in fruit production, 27% can be attributed to differences between regions. Most of this variation is the result of regional differences in inflorescence size, which in turn influence fruit production.

Why does *Yucca whipplei* produce such large inflorescences if so few fruits can be supported? Two relevant hypotheses are discussed: (1) the floral display is the result of selection for pollen dissemination at the expense of fruit set; and (2) the floral display is the result of selection for a bet-hedging strategy either to increase the probability of adequate pollination when pollinators are unusually rare, or to allow individuals to support more fruits when resources are unusually abundant.

Introduction

The relationship between reproductive success and resources expended on reproduction is influenced by a number of extrinsic

factors. In flowering plants, one of the most important extrinsic factors is the pollen vector. Numerous studies have examined the potential significance of intra- and interspecific competition for pollinators in the evolution of flowering plants. Competition for pollinators has been implicated in the evolution of floral morphology, chemistry and color (e.g. Faegri and vander Pijl 1971), flowering time (e.g. Mosquin 1971; Heithaus 1974; Frankie 1975; Schemske 1977; Waser 1978), floral arrangement (e.g. Willson and Rathke 1974; Willson and Price 1977; Stephenson 1979; Schemske 1980), the quantity, quality and rate of production of floral rewards (e.g., Heinrich and Raven 1972; Baker and Baker 1975; Brown and Kodric-Brown 1979), and breeding systems and reproductive strategies (e.g. Schaffer and Schaffer 1977, 1979; Willson 1979). Nevertheless, there have been few studies of the population dynamics of plants and their pollinators. For example, although quantitative information on the relationship between pollinator density and seed set is available for some fruit crops (McGregor 1959; Free 1970; Nishida 1963), essentially no data exist on the relationship between plant and pollinator densities and reproductive success of plant populations in nature. The objective of this study is to determine how pollinator availability influences fruit set and reproductive success in *Yucca whipplei* (Agavaceae).

Yucca whipplei is found primarily in chaparral, scrub or dry woodland communities in southern California and the Baja peninsula. It forms a low-growing perennial rosette which flowers once and then dies. There is considerable variation in growth form, which has been the basis of separation into up to 5 subspecies, 2 monocarpic and 3 clonal (Haines 1941; McKelvey 1947; Webber 1953). Blooming occurs in the spring or early summer, with plants producing large paniculate flower stalks, bearing from 100 to several thousand perfect flowers which open in progression from the bottom to the top of the panicle. The duration of bloom for individual plants varies from site to site, averaging around 10 days at the driest sites and 30 days in more mesic areas. Fruit development on the lower portion of the panicle may begin while the upper portion is still flowering. Fruits typically take about a month to reach full size, dehiscing in the late summer or early fall. Each fruit contains 150 to 250 seeds. Seeds are dispersed by wind.

The yucca moth, *Tegeticula maculata*, is the only significant pollinator of *Y. whipplei* (Wimber 1958; Powell and Mackie 1966; Aker and Udovic 1981). *T. maculata* is also a highly specialized pre-dispersal seed predator. Female moths oviposit in the ovaries of fresh flowers and then actively pollinate the flowers, assuring food for their offspring (Riley 1892; Trelease 1893). Developing larvae feed on a small number of seeds. In late

Table 1. Characteristics of the 18 study sites

Site	Years studied	Location	Community-type	Elev. (M)	Subspecies of <i>Y. whipplei</i>
San Gabriel Foothills					
DS1	1978	Devil's Punchbowl	Desert scrub	1,250	caespitosa (clonal)
DS2	1978	Valyermo	Desert scrub	1,075	caespitosa
DS3	1978	Acton	Desert scrub	900	caespitosa
Peninsular Ranges					
CSS1	1978	Cardiff	Coastal sage scrub	30	typica (solitary)
CSS2	1978-1979	Cardiff	Coastal sage scrub	60	typica
CSS3	1978-1979	San Diego	Coastal sage scrub	250	typica
CSS4	1978-1979	Escondido	Coastal sage scrub	250	typica
CSS5	1978	Santiago Canyon	Coastal sage scrub	350	typica
Santa Rosa - San Jacinto Mountains					
CH1	1978	Valle Vista	Evergreen Chaparral	850	typica
CH2	1978	Palm Canyon	Evergreen Chaparral	1,200	typica
CH3	1978-1979	Pinyon Flat	Evergreen Chaparral	1,200	typica
CH4	1979	Pinyon Flat	Evergreen Chaparral	1,200	typica
Southeastern San Gabriels: Lone Pine Canyon					
LPC1	1978	Lone Pine Canyon	Evergreen Chaparral	1,000	caespitosa
LPC2	1978	Lone Pine Canyon	Evergreen Chaparral	1,100	caespitosa
LPC3	1978	Lone Pine Canyon	Evergreen Chaparral	1,240	caespitosa
LPC4	1978	Lone Pine Canyon	Evergreen Chaparral	1,380	caespitosa
LPC5	1978	Lone Pine Canyon	Evergreen Chaparral	1,600	caespitosa
LPC6	1978	Lone Pine Canyon	Evergreen Chaparral	1,800	caespitosa

summer or early fall they leave the pods and drop to the soil, where they overwinter. Emergence of adult moths is scattered throughout the blooming season, with individual moths living for approximately one week (Aker, pers. comm.). Powell and Mackie (1966) detail the natural history of *T. maculata*, and Aker and Udovic (1981) provide a summary and analysis of behavior associated with oviposition and pollination.

My observations of *Y. whipplei* during the flowering and fruiting seasons at a number of locations, together with observations of other investigators (Powell and Mackie 1966; Schaffer and Schaffer 1977), indicate that (1) only a small fraction of the flowers on an inflorescence produce mature fruits and (2) the number of mature fruits increases with inflorescence size. Two alternative hypotheses have emerged to explain these observations. The first hypothesis, which I will call the pollinator-limitation hypothesis, can be stated as follows: (1) fruit set is limited by pollinator availability, (2) pollinators visit larger inflorescences more frequently than smaller inflorescences, and therefore (3) larger inflorescences produce more fruits (Schaffer and Schaffer 1977, 1979). The second hypothesis, the resource-limitation hypothesis, can be stated as follows: (1) because of resource limitations, inflorescences can support a limited number of fruits (the sustainable fruit number); (2) the sustainable fruit number of any inflorescence is much less than the number of flowers produced; (3) because both the sustainable fruit number and inflorescence size are positively related to the amount of resources available for reproduction, fruit production and inflorescence size should be positively correlated; (4) typically, the number of flowers fertilized on an inflorescence exceeds the sustainable fruit number; and (5) regulation of fruit production at a sustainable level is achieved by abortion of excess fruits (Udovic and Aker 1981). Hence pollinators are not limiting. Distinguishing between these hypotheses is essential to understanding the population dynamics and coevolution of *Yucca whipplei* and its pollinator.

To test the pollinator-limitation and resource-limitation hypotheses, I have obtained estimates of pollinator availability, inflorescence size and fruit number for a number of plants at various locations over a two-year period. Observed relationships between these variables, both within and between sites, are compared with the predictions of the two hypotheses.

Study Sites

This study was conducted in southern California during the spring and summer of 1978 and 1979 at the 18 locations shown in Fig. 1. Using the classification scheme of Munz and Keck (1959, see Munz 1973), I have grouped these sites according to geographic location and plant community-type (Table 1). Three sites (DS1-DS3) are located in the northern foothills of the San Gabriel mountains on the southwestern margin of the Mohave desert. Elevation at these sites ranges from 900 m to 1,250 m. Vegetation is a mixture of species characteristic of Joshua tree woodland, sagebrush scrub, pinyon-juniper woodland (Munz 1973) and California juniper woodland communities (as described by Vasek and Thorne (1977) (*Yucca brevifolia*, *Juniperus californica*, *Artemisia tridentata*, *Chrysothamnus nauseosus*, *Purshia* spp., etc.)). For the purposes of this paper, these mixed communities are labelled desert scrub (Table 1). The 5 sites (CSS1-CSS5) located in the southern peninsular ranges (Fig. 1) are characterized by their relatively low elevation (30 to 350 m) and by drought-deciduous species typical of coastal sage scrub communities (*Artemisia californica*, *Salvia* spp., *Eriogonum fasciculatum*, *Encelia californica*, etc.). The 4 (CH1-CH4) sites in the San Jacinto-Santa Rosa mountains are at high elevations (850 to 1,200 m) and are dominated by evergreen sclerophyllous species typical of chamise or redshank chaparral (*Adenostoma fasciculatum*, *A. sparsifolium*, *Arctostaphylos* spp., *Ceanothus* spp., *Quercus* spp., etc.).

At the sites in the peninsular ranges and the Santa Rosa

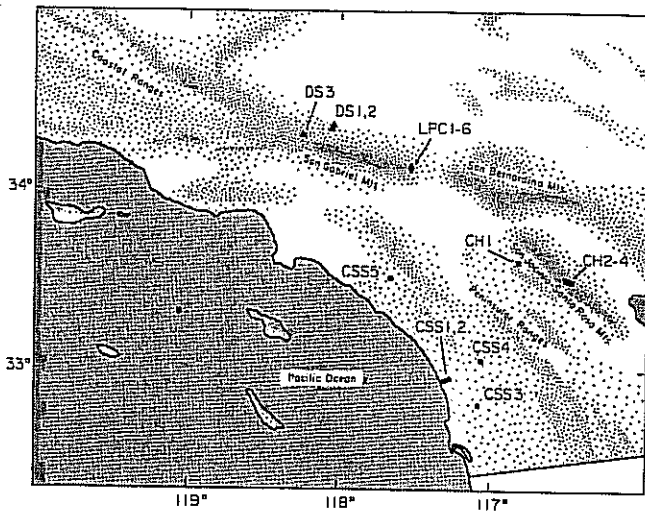


Fig. 1. Map of southern California showing the location of study sites relative to major land formations

mountains (CCS and CH), *Y. whipplei* has a monocarpic growth form (ssp. *typica*). However, at the 3 desert scrub sites north of the San Gabriels, the plants are clonal (ssp. *caespitosa*). Each individual plant consists of a number of rosettes connected by short above-ground branches (Haines 1941). Although the entire clump of rosettes may flower many times over a period of years, each rosette flowers only once and then dies.

Incomplete data were gathered in 1978 at 6 sites in Lone Pine Canyon, located near Cajon Pass in the southeastern portion of the San Gabriel mountains (LPC1-LPC6). The sites were located along an elevational transect ranging from 1,000 m to 1,800 m in a characteristic evergreen chaparral community, dominated by *Adenostoma fasciculatum*. *Yucca whipplei* has a clonal (ssp. *caespitosa*) growth form at these sites.

Methods

Estimates of pollinator availability, size of inflorescence and numbers of fruits set were obtained for all blooming plants within arbitrarily defined boundaries at as many sites as possible. Data were gathered at 11 sites in 1978 (Table 1). Four of these sites (CSS2, CSS3, CSS4, CH3) were also studied in 1979, as well as one new site (CH4). Data on inflorescence size and fruit set (but not pollinator availability) were also obtained for the Lone Pine Canyon sites in 1978.

Two measures of the size of the inflorescences of individual plants were obtained: 1) the height of the flowering stalk at maturity, and 2) the total number of flowers produced. The latter measure was obtained by counting the number of flower pedicels on each inflorescence after the completion of flowering.

To assess pollinator availability, the size of the adult population of *T. maculata* was estimated at each site at periodic intervals throughout the blooming season. Behavioral observations indicate that adult moths spend virtually all of their time in or around open flowers on inflorescences of *Y. whipplei*. By examining a large portion of the open flowers at a site, accurate population estimates were obtained without excessively disturbing the moths. Error estimates for these values were obtained by assuming that adult moths are distributed randomly among all of the open flowers at a site (i.e., the number of moths in an open flower is a Poisson variate). Several other approaches, based on different assumptions about the distribution of adult moths yielded similar variance estimates. An estimate for the total number of moth-days at each study site was obtained by weighting the estimates for each sample by the number of days since the previous sample and summing over the flowering season. Estimates for the variances for the total number of moth-days were obtained

similarly, taking advantage of the fact that the variance of a sum of stochastically independent random variables is equal to the sum of the variances.

The error estimates which result from these calculations are quite low; standard errors for total number of moth-days per flowering plant are about 5% of the estimated number of moth-days. However, several sources of error are not included in the calculations of these error statistics. For example, neither the error in estimating the total number of open flowers at a site on a given sampling date, nor the error in estimating the number of flowers actually checked for moths is included in the calculations. Furthermore, since only female moths pollinate, using the number of moth-days per blooming plant as a comparative measure of pollinator availability implicitly assumes similar sex ratios at all sites and introduces a potentially important source of error. Obtaining reliable estimates of the sex ratio was usually not possible because of difficulties in determining the sex of the moths without disturbing them. These non-calculable sources of error are probably more important than the error due to sampling, but it is unlikely that they are large enough to alter the interpretation of the results presented in the next section.

Sampling usually was not extensive or frequent enough to estimate accurately the number of visits by pollinators to individual plants over the blooming period. However, based on the number of open flowers at each census and the number of moths in the entire population at each census, an index of the expected number of visits by pollinators can be calculated for each plant using the formula:

$$V_i = \sum_{j=1}^n M_j \frac{F_{ij}}{\sum_{k=1}^n F_{kj}} \cdot d_{j-1,j} \quad (1)$$

where V_i is the visitation index for plant i , M_j is the number of moths in the population at the j^{th} census, F_{ij} is the number of open flowers on plant i at the j^{th} census and $d_{j-1,j}$ is the number of days between the j^{th} census and the previous one. The index assumes that for a given number of moths, the number of visits to a given plant in an interval will be proportional to the fraction of open flowers in the population which belong to that plant. Regressions of the number of moths found on individual inflorescences vs the number of open flowers on the inflorescence for each census at several sites lead strong support for this assumption (Aker unpubl.).

Fruit set was estimated by counting the number of fruits for each plant at each site several weeks after the end of the blooming period. The counts were made after the plants had aborted excess immature fruits (Udovic and Aker 1981) but before the period when most seed and fruit predation by vertebrates and insects occurs. Hence the counts are estimates of the number of mature fruits which each plant would have produced in the absence of predation. Because abortion of immature fruits is common in *Y. whipplei*, counts of mature fruits do not necessarily provide accurate estimates of the number of fertilized flowers.

Counts of the number of seeds per fruit for 20 plants at 7 sites indicate that the number of fruits is an excellent predictor of seed set. Although the differences between plants and between sites in the number of seeds per fruit are statistically significant (unpubl.), almost all of the variation in the total number of seeds produced by individual plants can be accounted for by variation in the number of fruits produced ($r^2=0.95$).

Results

Variation in Mean Fruit Production Between Populations

The mean values for the number of flowers, stalk height, the number of mature fruits, and fruit set (the percentage of flowers producing mature fruits) for each population, together with estimates of the abundance of pollinators, are presented in Table 2. As preliminary observations indicated, fruit set in *Yucca whipplei* is low, usually below 10%. The values for mean fruit

Table 2. Means and standard errors (sample size in parenthesis) for measurements of inflorescence size, pollinator availability and fruit number and mean and 95% confidence limits for fruit set for each population

Site	Year	\bar{X} stalk height	\bar{X} # flowers	Moth-days/ plant	\bar{X} visitation index	\bar{X} # fruits	\bar{X}^a fruit set (%)	95% ^a confidence limits
Northern Foothills of San Gabriels (desert scrub)								
DS1	1978	259 ± 10 (28)	1,032 ± 143 (16)	11 ± 0.9	11 ± 2.7 (17)	19 ± 8 (17)	0.1	0.0–0.5 (15)
DS2	1978	222 ± 8 (48)	612 ± 97 (22)	0.5 ± 0.1	1.6 ± 0.4 (15)	28 ± 4 (47)	3.0	1.5–7.2 (22)
DS3	1978	206 ± 7 (38)	1,151 ± 112 (14)	1.6 ± 0.2	2.8 ± 0.5 (15)	32 ± 5 (38)	1.3	0.7–2.6 (14)
Pooled regional mean		225 ± 10 (114)	886 ± 74 (52)	3.7	6 ± 1 (47)	28 ± 3 (102)	1.0	0.8–1.3 (51)
Mean of population means		229 ± 16 (3)	932 ± 163 (3)	4.4 ± 3.3 (3)	5 ± 3 (3)	26 ± 4 (3)	1.5	0.0–3.1 (3)
Peninsular Coastal Ranges (coastal sage scrub)								
CSS1	1978	275 ± 6 (49)	971 ± 72 (17)	1.6 ± 0.3	1.5 ± 0.1 (40)	36 ± 5 (47)	0.4	0.1–1.2 (17)
CSS2	1978	273 ± 6 (65)	1,071 ± 83 (38)	29 ± 0.9	35 ± 2 (64)	98 ± 6 (64)	7.0	4.8–11.0 (38)
CSS2	1979	316 ± 8 (50)	1,199 ± 75 (37)	80 ± 3	79 ± 6 (44)	105 ± 8 (50)	6.2	4.2–9.8 (37)
CSS3	1978	268 ± 6 (51)	877 ± 100 (20)	106 ± 2	88 ± 10 (51)	92 ± 6 (51)	9.4	7.1–12.9 (20)
CSS3	1979	279 ± 8 (40)	1,054 ± 77 (38)	149 ± 3	153 ± 17 (40)	112 ± 10 (40)	6.2	3.7–11.9 (38)
CSS4	1978	259 ± 6 (85)	1,043 ± 112 (12)	83 ± 2	80 ± 5 (82)	88 ± 5 (83)	6.9	4.8–10.4 (12)
CSS4	1979	269 ± 5 (54)	1,001 ± 51 (47)	270 ± 6	268 ± 22 (52)	96 ± 7 (55)	9.0	8.1–10.1 (47)
CSS5	1978	246 ± 9 (43)	926 ± 92 (18)	103 ± 2	90 ± 14 (41)	80 ± 8 (42)	4.7	2.4–11.6 (18)
Pooled regional mean		272 ± 2 (437)	1,035 ± 29 (227)	99	98 ± 5 (414)	89 ± 3 (432)	5.3	4.7–6.0 (227)
Mean of population means		273 ± 7 (8)	1,018 ± 35 (8)	103 ± 29 (8)	99 ± 29 (8)	88 ± 8 (8)	6.2	4.2–8.2 (8)
Santa Rosa-San Jacinto Mountains (evergreen chaparral)								
CH1	1978	288 ± 6 (53)		92 ± 2	90 ± 6 (28)	88 ± 7 (53)	—	—
CH2	1978	293 ± 9 (30)		258 ± 3	253 ± 26 (14)	127 ± 12 (30)	—	—
CH3	1978	315 ± 7 (43)	2,259 ± 122 (43)	145 ± 3	145 ± 8 (43)	178 ± 17 (43)	5.4	3.5–8.9 (43)
CH3	1979	324 ± 8 (46)	2,045 ± 111 (46)	84 ± 2	84 ± 6 (46)	182 ± 15 (46)	6.7	4.8–9.8 (46)
CH4	1979	313 ± 7 (62)	1,665 ± 83 (62)	71 ± 2	71 ± 3 (62)	156 ± 10 (62)	8.7	7.8–9.8 (62)
Pooled regional mean		306 ± 4 (234)	1,913 ± 56 (151)	116	107 ± 5 (193)	146 ± 6 (234)	6.9	5.7–8.5 (151)
Mean of population means		307 ± 7 (5)	1,990 ± 174 (3)	130 ± 34 (5)	128 ± 34 (5)	146 ± 18 (5)	6.9	5.0–8.8 (3)
San Gabriels: Lone Pine Canyon (evergreen chaparral)								
LPC1	1978	321 ± 9 (20)				166 ± 14 (20)		
LPC2	1978	329 ± 12 (20)				163 ± 31 (20)		
LPC3	1978	350 ± 10 (19)				233 ± 21 (20)		
LPC4	1978	355 ± 14 (11)				244 ± 39 (11)		
LPC5	1978	370 ± 16 (17)				254 ± 27 (18)		
LPC6	1978	342 ± 11 (20)				84 ± 17 (20)		
Pooled regional mean		343 ± 5 (107)				185 ± 10 (109)		
Mean of population means		345 ± 7 (6)				191 ± 27 (6)		

Pooled regional means are calculated using the plant as the sample unit. Means of the population means are calculated using the population as the sampling unit

^a Mean and confidence limits of fruit set are calculated by back transforming values obtained using the arcsine transformation. Because the arcsine transformation emphasizes the lower values, mean values are typically 2–3% lower than means calculated from untransformed data

set appear remarkably uniform, particularly when contrasted with the amount of variation in the mean values of each of the other variables. Analysis of variance (using the arcsine transformation) indicates significant differences between populations in mean fruit set ($p < 0.001$). However, with the exception of the three desert scrub populations and CSS1, where means for fruit set were 3% or below, all populations belong to one homogenous subset with mean fruit set varying from 4.7% at CSS5 in 1978 to 9.4% at CSS3 in 1978 (Duncan's multiple range test, with 5% significance level used as a criterion for homogeneity). Any comprehensive explanation of variation in fruit number between plants should account both for the low values of fruit set and for the relative constancy of mean fruit set between populations.

Mean inflorescence size, mean fruit number and the abundance of pollinators all vary considerably between populations (Table 2). The pollinator-limitation hypothesis predicts that the mean number of fruits per plant should be positively correlated with the number of moth-days per plant (an index of pollinator abundance at each population), while the resource-limitation hypothesis predicts that the mean number of fruits per plant should be positively correlated with the average inflorescence size (mean stalk height or mean number of flowers). If pollinator abundance were strongly correlated with measures of inflorescence size, it might be difficult to distinguish between the two hypotheses. However, the number of moth-days per plant varies discordantly with inflorescence size (although moth-days is positively correlated with mean stalk height ($r^2 = 0.14$, $p > 0.10$) and

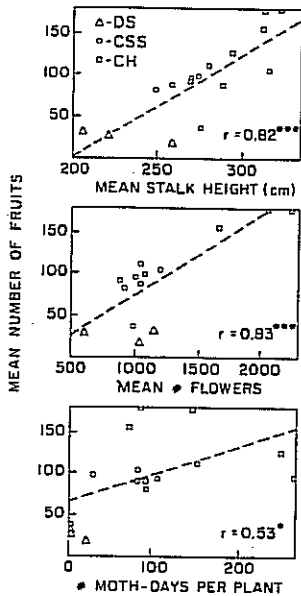


Fig. 2a-c. Between-site correlations of mean number of fruits and (a) mean stalk height, (b) mean number of flowers, and (c) number of moth-days per plant

the mean number of flowers ($r^2=0.05$, $p>0.25$), neither correlation is significant, and both are largely due to the low values of all three variables in the three desert scrub sites; hence the two hypotheses yield divergent predictions.

Mean stalk height and mean number of flowers are excellent predictors of the mean number of fruits produced, whereas the abundance of pollinators is a relatively poor predictor. The regressions for the mean number of fruits with mean stalk height (Fig. 2a) and the mean number of flowers (Fig. 2b) are highly significant ($r^2=0.68$, $p<0.001$; $r^2=0.69$, $p<0.001$, respectively). If the LPC sites are included in the regression on stalk height, $r^2=0.73$. The LPC sites were not included in Figure 2 since no data were available for pollinator availability. There is also a significant positive relationship between the mean number of fruits and the number of moth-days per plant (Fig. 2c; $r^2=0.26$, $p<0.05$). However, the latter explains a significantly smaller portion of variance in the mean number of fruits. Furthermore, this correlation appears to be a consequence of the low values of both of these variables at the desert scrub sites and at one coastal sage scrub site (CSS1). If these sites are excluded from analysis, the regression becomes insignificant ($r^2=0.004$), whereas the regressions of the mean number of fruits on mean stalk height and mean number of flowers remain highly significant ($r^2=0.68$ and 0.94 , respectively). Although the number of moth-days per plant varies by almost an order of magnitude between the populations of the coastal sage scrub and chaparral sites, this variable has no effect on the mean number of fruits in these populations. Hence although pollinators may be limiting at the desert scrub study sites and at one of the coastal sage scrub sites (CSS1), they are not the limiting factor in fruit production in the coastal sage scrub or chaparral. Despite an apparent excess of pollinators fruit set is still low, and the mean number of fruits matured is closely correlated with the average size of inflorescence. These observations are consistent with the resource-limitation hypothesis.

Between-year comparisons of mean fruit production at four sites which were studied in both 1978 and 1979 provide further

Table 3. Analyses of variance for mean stalk height, mean number of flowers, number of moth-days per plant, and mean number of fruits, by region. Moth-days was transformed using the log transformation to reduce heterogeneity in the variance between regions

Dependent variable	Source of variation	d.f.	r^2	F-value
\bar{X} stalk height	Region	2	0.68	14.0***
	Residual	13	0.32	
\bar{X} flowers	Region	2	0.85	31.8***
	Residual	11	0.15	
In moth-days	Region	2	0.55	8.1**
	Residual	13	0.45	
\bar{X} fruits	Region	2	0.73	17.9***
	Residual	13	0.27	

evidence for the resource-limitation hypothesis (Table 2). At each site there was little change in either mean stalk height or mean number of flowers, with the exception of CSS2, where mean stalk height was significantly greater in 1979 ($p<0.001$). At all four sites, however, the number of moth-days per plant in 1979 differed significantly from 1978, with increases of $1.4\times$ at CSS3, $2.7\times$ at CSS2, $3.3\times$ at CSS4 and a decrease of $0.58\times$ at CH3 (in all cases $p<0.001$). Despite the large change in pollinator availability, however, differences in the mean number of fruits between years were not significant at any of the sites. At each of the sites (including CH3, where pollinator availability decreased) the mean number of fruits was slightly higher in 1979 ($1.02\times$ at CH3, $1.07\times$ at CSS2, $1.11\times$ at CSS4 and $1.22\times$ at CSS3).

Much of the variation between sites in the average size of inflorescence and in the mean number of mature fruits can be attributed to regional differences (Table 3). Mean stalk height, mean number of flowers, and mean number of fruits show parallel trends (Table 2): values are lowest for populations located in the xeric desert scrub communities in the northern foothills of the San Gabriels; intermediate for the coastal sage scrub populations of the peninsular ranges where moisture levels are probably also intermediate; and highest for those populations in the relatively mesic evergreen chaparral (Harrison et al. 1971) in the San Jacinto-Santa Rosa mountains and in the southeastern San Gabriels. While the numbers of moth-days per plant in the desert scrub region are significantly lower than in the other regions, there is no significant difference between the coastal sage scrub and chaparral ($t=0.97$; d.f.=11). These results are consistent with the hypothesis that differences between regions, perhaps in the availability of water, influence the amount of resources available for reproduction in *Yucca whipplei*, which is reflected in regional differences in inflorescence size and in the number of mature fruits that a plant can support.

Variation in Fruit Production Within Populations

The pollinator-limitation hypothesis yields the following predictions about the relation between pollinator availability, inflorescence size (stalk height or number of flowers) and fruit number within each study site: (a) the number of fruits produced by each plant should be positively correlated with the number of visits by pollinators; (b) the number of visits by pollinators should be positively correlated with inflorescence size; and (c) the number of fruits should be positively correlated with inflorescence size. The latter is also a prediction of the resource-limita-

Table 4. Correlation coefficients (sample sizes in parentheses) for relationships between fruit set, inflorescence size and expected pollinator visits for each study site. Unless noted otherwise, values are significant at the 0.001 level

Site	Year	# fruits vs. visitation index	# fruits vs. stalk height	# fruits vs. # flowers	Visitation index vs. stalk height	Visitation index vs. # flowers
San Gabriel Foothills						
DS1	1978	-0.23 ^(ns) (17)	0.32 ^(ns) (17)	0.24 ^(ns) (15)	0.53* (17)	0.76 (15)
DS2	1978	0.23 ^(ns) (15)	0.33* (47)	0.52** (22)	0.30 ^(ns) (15)	0.53 ^(ns) (10)
DS3	1978	0.41 ^(ns) (15)	0.13 ^(ns) (38)	0.74 (14)	0.36 ^(ns) (15)	0.97 ^(ns) (3)
Peninsular Ranges						
CSS1	1978	0.05 ^(ns) (40)	0.33* (47)	0.58** (17)	-0.04 ^(ns) (40)	-0.08 ^(ns) (15)
CSS2	1978	0.58 (64)	0.55 (64)	0.87 (38)	0.44 (64)	0.67 (38)
CSS2	1979	0.62 (44)	0.55 (50)	0.69 (37)	0.59 (44)	0.77 (37)
CSS3	1978	0.54 (51)	0.54 (51)	0.64 (20)	0.32** (51)	0.76 (20)
CSS3	1979	0.58 (39)	0.56 (40)	0.77 (38)	0.35* (39)	0.74 (38)
CSS4	1978	0.46 (82)	0.47 (82)	0.78 (12)	0.34 (82)	0.83 (12)
CSS4	1979	0.66 (52)	0.39** (54)	0.59 (47)	0.44 (51)	0.52 (47)
CSS5	1978	0.56 (41)	0.60 (42)	0.76 (18)	0.61 (41)	0.79 (18)
Santa Rosa-San Jacinto Mts.						
CH1	1978	0.55 (28)	0.35** (53)		0.37* (28)	
CH2	1978	0.65** (14)	0.52** (30)		0.87 (14)	
CH3	1978	0.11 ^(ns) (43)	0.56 (43)	0.34* (43)	0.39 (43)	0.55 (43)
CH3	1979	0.70 (46)	0.63 (46)	0.70 (46)	0.44 (46)	0.87 (46)
CH4	1979	0.72 (62)	0.63 (62)	0.62 (62)	0.46 (62)	0.76 (62)
Southeastern San Gabriels						
LPC1	1978		0.40 ^(ns) (20)			
LPC2	1978		0.71 (20)			
LPC3	1978		0.66 (19)			
LPC4	1978		0.27 ^(ns) (11)			
LPC5	1978		0.67 (17)			
LPC6	1978		0.45* (20)			

ns=not significant

* $p < 0.05$; ** $p < 0.01$

tion hypothesis, which holds that the number of fruits a plant can support is an increasing function of the amount of resources spent on reproduction. Furthermore, since the resource-limitation hypothesis makes no specific predictions about the relationship between the number of visits by pollinators and other variables, predictions (a) and (b) of the pollinator-limitation hypothesis are also consistent with the resource-limitation hypothesis.

The three predictions of the pollinator-limitation hypothesis are all satisfied in 11 of 16 cases (Table 4). In 3 of the remaining 5 cases (DS2-78, CSS1-78 and CH3-78) there are significant positive correlations of the number of fruits with both measures of inflorescence size (prediction c), but no significant correlation of the number of fruits with the pollinator visitation index. In the two remaining cases (DS1-78 and DS3-78), sample sizes are low and the correlations of the number of fruits with the two measures of inflorescence size are positive but not significant ($p > 0.05$; one exception is the correlation between number of fruits and number of flowers at DS3-78, with $p < 0.001$). Correlations of the number of fruits with the pollinator visitation index at these 2 sites are also insignificant. At the Lone Pine Canyon sites, where only stalk height and the number of fruits were measured, fruit production was positively correlated with stalk height at all 6 sites (although correlations were significant at only 4 sites).

To analyze the relative influence of inflorescence size and pollinator visits on fruit production, multiple regressions of fruit production as a function of stalk height and visitation index

were obtained for all 16 populations with complete data (Table 5). The number of flowers was excluded from analysis because the sample sizes would have been significantly reduced at many of the sites where flowers were counted for a relatively small number of inflorescences. After adjusting for stalk height, the visitation index explains a significant amount of the remaining variation in fruit number at 9 of the 16 populations. After adjusting for visitation index, stalk height explains a significant portion of the remaining variation in 12 of the 16 populations.

Interpretation of these results depends on the adequacy of stalk height as a measure of the resources available to support developing fruits and of the visitation index as a measure of the actual number of visits by pollinators. If the correspondence between stalk height and reproductive expenditure is strong, then the variation in fruit production explained by the visitation index after adjusting for stalk height could confidently be attributed to variation in pollinator visits, rather than to some other component of reproductive expenditure correlated with the visitation index (e.g., duration of bloom of the inflorescence). Likewise, if the actual number of visits corresponds well with the visitation index, then the variation in fruit production explained by stalk height after adjusting for the visitation index could be confidently attributed to variation in the amount of resources available to support fruits. The adequacy of stalk height can be at least partially assessed by comparing the results of multiple regressions including the number of flowers as an independent variable with multiple regressions excluding it. For six popula-

Table 5. Multiple regression analyses of the number of fruits as a function of stalk height and the visitation index, for each population

Population	N	Partial Regression Coefficients			r ²			
		Constant	Height (cm)	Vis index	Total ^a	Height ^b	Vis index ^c	Vis index ^d
DS1-78	17	- 39.8	0.30	-1.67	0.32	0.26*	0.21	
DS2-78	15	- 50.5	0.37	2.10	0.25	0.20	0.01	
DS3-78	15	- 24.0	0.21	7.77	0.19	0.02	0.11	
CSS1-78	40	- 34.1	0.24	2.10	0.11	0.11*	0.00	
CSS2-78	64	- 51.6	0.37	1.40	0.44***	0.11***	0.14***	
CSS2-79	44	- 65.1	0.38	0.65	0.48***	0.09**	0.10**	0.00
CSS3-78	51	- 46.8	0.43	0.26	0.44***	0.15***	0.15***	
CSS3-79	39	- 67.2	0.41	0.25	0.48***	0.15**	0.17**	0.00
CSS4-78	82	- 36.9	0.39	0.31	0.32***	0.11***	0.10***	
CSS4-79	51	1.5	0.18	0.18	0.42***	0.01	0.27***	0.14***
CSS5-78	41	- 55.3	0.42	0.34	0.43***	0.12**	0.05	
CH1-78	28	- 92.5	0.43	0.64	0.44***	0.14*	0.14*	
CH2-78	14	- 6.2	0.07	0.43	0.42*	0.00	0.09	
CH3-78	43	-251.9	1.50	-0.28	0.34***	0.32***	0.01	0.01
CH3-79	46	-168.0	0.74	1.31	0.62***	0.13***	0.22***	0.06*
CH4-79	62	-110.5	0.52	1.51	0.64***	0.12***	0.23***	0.13***

^a Significance levels indicate overall significance of the multiple regression

^b Adjusted for vis index

^c Adjusted for height

^d Adjusted for height and flowers

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

tions with the most complete flower counts, Table 5 presents the proportion of variation in fruit number explained by the visitation index (1) after adjusting for stalk height only, and (2) after adjusting for both stalk height and the number of flowers. In five cases the visitation index explained a significant amount of variation after adjusting for stalk height. In all five cases, the proportion of variation explained by the visitation index was significantly less after adjusting for both stalk height and the number of flowers, suggesting that much of the explained variation attributed to the visitation index is likely to be due to covariation with components of reproductive expenditure other than stalk height.

The adequacy of the visitation index as a measure of pollinator visits is equally difficult to ascertain. Schaffer and Schaffer (1977, 1980) suggest that larger inflorescences will attract disproportionately more pollinators than smaller inflorescences. If they are correct, the number of pollinator visits to an inflorescence will be a nonlinear (accelerating) function of reproductive expenditure. The visitation index, on the other hand, is essentially linearly related to reproductive expenditure (eq. 1). In such a case, the variation in fruit production attributed to stalk height after adjusting for the visitation index could alternatively be due to an inherent non-linearity in the relationship between fruit production and the number of visits. To test for this, plots of the residuals of the regressions of fruit production on visitation index were examined for non-linear trends. None were detected. To further test for non-linearity, polynomial regressions of fruit production with (1) the visitation index and its square term, and (2) stalk height and its square term were obtained for all 16 populations. In every case, after adjusting for the linear term, the square term failed to explain a significant portion of the remaining variance in fruit number. Hence it is unlikely that the observed relationship between stalk height and fruit production is due to any correlation with a non-linear effect of visitation index.

Although strong correlations between independent variables within populations make interpretation of the correlation and

regression analyses difficult, cautious conclusions about the variation in fruit production within populations can be drawn: (1) with the exception of the desert scrub sites, there is a strong relationship between inflorescence size and fruit production in every population; (2) only part of this relationship can be attributed to covariation between inflorescence size and the visitation index. Even after adjusting for the visitation index, inflorescence size usually explains a significant portion of the variation in fruit production; (3) the role of pollinators in explaining variability in fruit production is more difficult to ascertain. Although in many populations the visitation index explains a significant portion of the variance in fruit number after adjustment for inflorescence size, this could be due to covariation with aspects of reproductive expenditure other than inflorescence size; (4) although values for fruit set are lowest and pollinators are probably limiting at the desert scrub study sites and at CSS1, it is at these sites that the predictions of the pollinator-limitation hypothesis are not satisfied. In part this may be due to low sample sizes. However, when pollinators are rare, factors other than inflorescence size, such as the spatial and temporal dispersion of emerging moths, may be more important in determining which inflorescences are visited by pollinators; (5) although there is considerable variation between populations in the functional relationships between fruit production and inflorescence size and the visitation index (Table 5), the similarity in functional relationships is equally striking, particularly within each region. This will be discussed in more detail in the next section.

A Comprehensive Analysis of Covariance

The results of an analysis of covariance of the number of fruits produced by individual plants are summarized in Table 6 and Fig. 3. Six independent variables were included in this analysis: region, study site, year, stalk height, number of flowers, and the visitation index. Complete data were available for 404 plants from 14 populations. To sort out interrelations between variables from the direct effects of each of these variables on the number

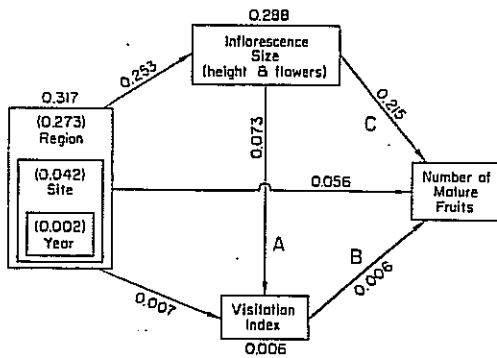


Fig. 3. Major causal links among the components of variation in the number of mature fruits produced by *Yucca whipplei*. The task of analysis is to determine what portion of the variance in mature fruits can be explained by each component and how that portion is partitioned among the various causal links. The pollinator-limitation hypothesis emphasizes links A and B, whereas the resource-limitation hypothesis emphasizes links C. Numbers represent coefficients of determination (r^2) obtained from analysis of covariance (Table 6)

of fruits, two different methods (hierarchical and classical) were used to partition the sums of squares. For the hierarchical method, independent variables were entered in a specified order, determined by the causal relationships between variables. For example, although region and site may affect inflorescence size, the converse is not true. Hence region and site were entered before inflorescence size. Likewise, inflorescence size may influence the number of pollinator visits, but not conversely. Hence stalk height and numbers of flowers were introduced before the visitation index. Sums of squares and significance levels were calculated by attributing to each independent variable the increment in the explained sums of squares due to the addition of that variable in the analysis. For the classical method, sums of squares and significance levels were calculated by attributing to each independent variable the increment in the sums of squares due to that variable if it were introduced after all other independent variables but before interactive effects. (However, since site and year were nested within region, these variables were always introduced after region). If all independent variables are orthogonal, the hierarchical and classical methods yield identical results. If the independent variables are intercorrelated, however, a comparison of the two approaches can be used to disentangle the effects of independent variables on each other from their direct effects on the response variable.

The following results emerge from this analysis (Fig. 3; Table 6):

(1) A total of 68.6% of the variance in fruit number between plants can be accounted for by the six variables considered and the interactive effects.

(2) Most of the variation between populations is due to variation between regions. Of the 31.7% of the variance attributed to region, site, and year when these variables are entered first, 27.3% is attributed to region. Differences between sites within region are statistically significant, but account for only 4.2% of the variance in fruit number. Differences between years within site are not significant.

(3) Most of the variation in fruit number due to region, site and year is due to the effects of these variables (particularly region) on the covariates (particularly inflorescence size). If the factor variables are entered after the covariates (as in the classical model) they account for only 5.6% of the variance, as opposed to 31.7% in the hierarchical model. The difference in these values

reflects the extent to which regional variation in fruit number parallels regional variation in inflorescence size and, to a lesser extent, the visitation index (Fig. 3).

(4) Inflorescence size is clearly the dominant independent variable in the analysis. In predicting the number of fruits produced by an inflorescence, information about the size of the inflorescence is far more useful than either information about location or information about the availability of pollinators. Height and flowers together account for 54.1% of the variation in fruit number if introduced first, 28.8% if introduced after region, site and year, and 21.5% of the variance if introduced after region, site, year and the visitation index.

(5) Although the number of visits by pollinators may significantly influence fruit production at a few locations, its overall influence, though statistically significant, is practically negligible. By itself, the visitation index accounts for 8.6% of the variation in fruit number. When introduced after the factors and other covariates, it accounts for only 0.6%, and ranks behind all other variables except year in its relative importance. Furthermore, the interaction between factors and the visitation index accounts for more variation than the visitation index itself, indicating that the actual relationship between visitation index and the number of fruits (after adjusting for the other covariates) varies considerably between populations.

(6) In contrast, the interaction between factors and stalk height, although statistically significant (indicating that the partial regression coefficient of fruit number vs. stalk height varies significantly between populations), accounts for only a small fraction of the variation due to stalk height itself. Furthermore, the interaction between factors and the number of flowers is not significant, implying uniformity between populations in the partial regression coefficient of fruit number vs. flowers. This, of course, is simply a reflection of the relative constancy of mean fruit set between populations.

Discussion

The major results can be stated briefly as follows: (1) On the average, less than 10% of the flowers on an inflorescence of *Yucca whipplei* produce mature fruits. Variability in the percentage of flowers producing mature fruits is low both within and between study sites. (2) There are strong positive correlations of fruit production with inflorescence size, both within sites and between sites. More than half of the variability in fruit production among plants can be explained by inflorescence size. (3) There are strong positive correlations of the expected number of pollinator visits with inflorescence size at most of the study sites, but inflorescence size and pollinator abundance vary discordantly between sites and between years. (4) There are strong positive correlations of fruit production with the expected number of visits by pollinators at most study sites, but there is only a weak relationship between fruit production and pollinator abundance between study sites. Overall, the expected number of pollinator visits explains only a small portion of the variation in fruit production. (5) In the four sites studied for two years, there was little change in average inflorescence size or fruit production from 1978 to 1979, despite large differences in pollinator abundance at each of the sites.

These findings, together with the results on fruit abortion presented by Udovic and Aker (1981), support the resource-limitation hypothesis. Udovic and Aker (1981) have demonstrated that fruit abortion serves to regulate fruit set in *Yucca whipplei*. Plants initiating more fruits than they can sustain abort the excess fruits. At their study sites (CH3 and CH4), the sustainable fruit

Table 6. Analysis of covariance of the number of fruits for individual plants from all study sites. The six independent variables include three nested factor variables: geographic area or community-type (REGION; see Table 1), study site (SITE), and year (YEAR); and three covariates: stalk height (HEIGHT), the number of flowers (FLOWERS) and the visitation index (VIS INDEX). Complete data were available for 404 plants. Sums of squares were partitioned using two alternative methods: (A) hierarchical and (B) classical. In the former, r^2 values and significance levels were calculated for each independent variable after adjusting for variables entered previously. In the latter case, each independent variable is evaluated as if it were entered after the other independent variables but before the interactive terms. For the classical model, r^2 values do not sum to unity because the independent variables are not orthogonal

A. Hierarchical model				B. Classical model			
Source of variation (order of entry)	d.f.	r^2	F	Source of variation	d.f.	r^2	F
Factors				Factors			
REGION (1)	2	0.273	151.7***	REGION (adj. for covariates)	2	0.028	15.6***
SITE (2; nested within REGION)	7	0.042	6.7***	SITE (nested within REGION)	7	0.027	4.3***
YEAR (3; nested within SITE)	4	0.002	0.5 ^(ns)	YEAR (nested within SITE)	4	0.001	0.3 ^(ns)
Total factors	13	0.317	27.1***	Total factors (adj. for covariates)	13	0.056	4.8***
Covariates				Covariates			
HEIGHT (4)	1	0.210	232.5***	HEIGHT	1	0.035	38.9***
FLOWERS (5)	1	0.078	86.2***	FLOWERS	1	0.053	58.4***
INFLORESCENCE SIZE (HEIGHT and FLOWERS)	2	0.288	160.1***	INFLORESCENCE SIZE (HEIGHT and FLOWERS)	2	0.215	119.5***
VIS INDEX (6)	1	0.006	7.0**	VIS INDEX	1	0.006	7.0**
Total covariates	3	0.294	108.9***	Total Covariates (adj. for factors)	3	0.294	108.9***
Factors and covariates	16	0.611	42.4***	Factors and Covariates	16	0.611	42.4***
Factor-covariate interaction				Factor-covariate interaction			
FACTORS*HEIGHT (7)	13	0.025	2.1*	FACTORS*HEIGHT	13	0.030	2.7**
FACTORS*FLOWERS (8)	13	0.018	1.6 ^(ns)	FACTORS*FLOWERS	13	0.016	1.5 ^(ns)
FACTORS*VIS INDEX (9)	12	0.032	3.0***	FACTORS*VIS INDEX	12	0.023	3.0***
Total interaction	38	0.075	2.2***	Total interaction (adj. for factors and covariates)	38	0.075	2.2***
Factors, covariates and interaction	54	0.686	14.1***	Factors covariates and interaction	54	0.686	14.1***
Residual	349	0.314		Residual	349	0.314	

set was about 10%, with over 90% of the inflorescences initiating fruits on more than 10% of their flowers. Hence the low fruit set of *Yucca whipplei* is not necessarily due to limitation of fruit production by pollinators. Indeed, the weak relationship of pollinator abundance and fruit production between sites and between years, contrasted with the strong correlation between inflorescence size and number of fruits suggests that pollinators are not limiting. The consistent values of mean fruit set of 5–9% at most study sites suggest that most inflorescences are producing the maximum number of fruits which they can sustain without reducing seed size, and the strong correlations between inflorescence size and fruit number suggest that large inflorescences can sustain more fruits than small inflorescences.

The desert scrub sites appear to be exceptions to several of the above conclusions. First, pollinators are rare at these sites. Moreover, my observations over several years indicate that *Tegeticula maculata* is rare throughout the northern foothills of the San Gabriel mountains. Second, mean fruit set is comparatively low at these sites (Table 2). 25% of the inflorescences produced no fruits. It is possible that the proportion of flowers capable of sustaining fruits is lower in the desert scrub than in the coastal sage scrub or chaparral owing to more extreme environmental conditions. However, an examination of 40 infructescences at DS2 and 40 infructescences at DS3 in August, 1979, suggests that fruit abortion is insignificant at these sites. Only 3 of the 80 infructescences had aborted more than one or two fruits. Hence, pollinators are probably the limiting factor in fruit production in this region.

Nevertheless, there is little evidence for the pollinator-limitation hypothesis from the desert scrub sites. Within-site correla-

tions between the number of fruits and inflorescence size are generally weaker than the correlations obtained at other study sites, and several are not significant (Table 2). Furthermore, there are no significant within-site correlations between the number of fruits and the visitation index. Although small sample sizes might explain why the predictions of the pollinator-limitation hypothesis fail to hold in the desert scrub sites, factors other than inflorescence size (such as the location of the inflorescence relative to the emergence of adult yucca moths or the timing of flowering) may be more important in determining which inflorescences are visited by the few available pollinators.

Although it is too early to evaluate the generality of the resource-limitation hypothesis, the results of other recent studies suggest that it may have broad applicability. Willson and Rathke (1974) and Willson and Price (1977) have argued that pollinators do not limit fruit production in *Asclepias* spp., even though the proportion of flowers producing mature fruits is low. Fruit abortion is apparently common in *Asclepias* and may serve the same regulatory function as in *Yucca whipplei*. Based on a series of artificial pollination experiments, Stephenson (1979) has reached similar conclusions for *Catalpa speciosa*, although he points out that pollinators may occasionally be limiting. Together with the results presented here, these studies suggest that other cases of low fruit set, often attributed to insufficient pollination, may actually result from a shortage of resources necessary to support fruit development on all of the flowers produced or fertilized (Lloyd 1979, 1980).

The resource-limitation hypothesis raises an important question about the floral display of *Y. whipplei*: why produce so many flowers when so few fruits can be supported? Indeed,

if flowers and fruits are competing for limited resources, reducing flower production might increase total fruit production. Willson and Rathke (1974) and Willson and Price (1977) have argued that the main selective advantage of excess flowers in *Asclepias* spp. is to increase the male component of fitness, pollen donation, rather than to increase the female component of fitness, fruit production. For simultaneous hermaphrodites such as *Asclepias* and *Yucca*, the observed reproductive strategy may represent the optimal compromise between the conflicting goals of maximizing the male and female components of fitness (Maynard Smith 1977; Willson 1979; Charnov 1979). Although no direct information is as yet available on pollen dissemination in *Y. whipplei*, the positive correlations between inflorescence size and the number of pollinator visits within study sites suggest that pollen dissemination increases with flower number. Hence, although reducing flower production might increase the sustainable fruit number, it might also reduce the amount of pollen disseminated.

Stephenson (1979) has provided a different explanation for the production of excess flowers by *Catalpa speciosa*. If pollinators are attracted to large inflorescences, excess flowers may serve as a buffer to increase the likelihood of visits by pollinators during years of low pollinator availability. Uncertainty in the availability of resources to support fruits might also select for a bet-hedging strategy. Excess flowers could allow plants to take advantage of occasional years of plentiful resources. Fruits which might otherwise be aborted would be able to complete development. Whether bet-hedging or selection for pollen donation can account for the 10-fold excess of flowers produced by *Y. whipplei* remains to be determined.

These results pertain to another important question about the reproductive strategy of *Yucca whipplei*: why do individual rosettes flower only once and then die? Observations by Schaffer and Schaffer (1977, 1979) indicate that (1) the amount of time spent by pollinators on an inflorescence increases disproportionately with increased size of the inflorescence in *Y. whipplei* and in many species of *Agave*, and (2) that fruit set also increases disproportionately with inflorescence size in these species. Based on models of the adaptive significance of semelparous vs. iteroparous reproductive strategies (Schaffer and Gadgil 1976; Schaffer 1979), and assuming a causal relationship between the number of pollinator visits and fruit production, Schaffer and Schaffer (1977, 1979) propose that the preference of pollinators for larger inflorescences has been an important selective force in the evolution of semelparous reproduction in these species. However, if the resource-limitation hypothesis is correct, then the number of pollinator visits has little influence on fruit production in *Yucca whipplei*. Perhaps its semelparous reproductive strategy also results from selection for increased pollen dissemination rather than increased fruit set.

The resource-limitation hypothesis has important consequences for understanding the population dynamics of mutualistic interactions. Mathematical models of mutualism (e.g., May 1976; Vandermeer and Boucher 1978; Goh 1979) have generally assumed that increasing the density of either population leads to an increased growth rate of the other, resulting in a destabilizing positive feedback loop. This has led some to conclude that the interaction between mutualists has a destabilizing effect on the dynamics of the system. However, in plant-pollinator interactions, if pollinators are not limiting, alterations in the density of pollinators (within limits) will not affect the growth rate of the plant population even though individual plants which attract more pollinators may have increased relative fitness due to increased pollen dissemination. In the case of yuccas and

yucca moths, an increase in the density of moths beyond the point of satiation in fruit set may actually result in an overall decrease in seed survival for the population because of increased predation by yucca moth larvae. Hence the mutualistic interaction could have a stabilizing effect on population dynamics, qualitatively resembling an exploitation (predator-prey) system. The possibility that other mutualistic interactions are stabilizing for similar reasons deserves further consideration.

I conclude by mentioning some important limitations of this study. First, although my findings are consistent with the resource-limitation hypothesis, comparative data on fruit initiation and fruit abortion rates from a number of study sites, coupled with attempts to increase fruit production by artificial pollination experiments, are necessary to conclusively test the resource-limitation hypothesis. Second, this study concentrates solely on the influence of pollinators on the reproductive ecology of *Yucca whipplei*. However, several other species, including insect flower and seed predators and vertebrate fruit and seed predators, appear to be major sources of fruit and seed mortality. Investigations of their importance to the reproductive ecology of *Y. whipplei* are crucial to the development of a comprehensive view of the factors influencing the evolution of the plant's reproductive strategy and floral display. Third, there is a need for detailed comparative studies of other species of yuccas and perhaps other closely related genera (e.g. *Agave*, *Nolina*, *Xerophyllum*), extending the work already done on pollination by Schaffer and Schaffer (1977, 1979) to other aspects of reproductive ecology.

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