Fruit Abortion and the Regulation of Fruit Number in *Yucca whipplei*

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Summary. Flowering and fruiting patterns of *Yucca whipplei* (Agavaceae), a monocarpic perennial of the southern California chaparral, were studied to determine the role of fruit abortion in the regulation of seed yield. Data on reproductive expenditure, fruit abortion and fruit maturation were obtained for 108 flowering individuals at two sites. The proportion of flowers maturing fruits was less than 10% at both sites. Inflorescences produced an average of 2,045 ± 111 and 1,743 ± 77 flowers at the two sites, initiated an average of 439 ± 48 and 304 ± 21 fruits, and matured an average of 194 ± 16 and 162 ± 10 fruits, respectively. Overall, 51% of the fruits which initiated development were aborted and abscized in an early stage of development.

The hypothesis that fruit abortion serves to regulate seed yield, matching fruit production to the available resources, yields three predictions which are borne out by our findings: (1) the proportion of initiated fruits which abort is an increasing function of the number of fruits initiated, (2) the number of fruits matured is an increasing function of estimates of the amount of resources available to support fruits, and (3) on any inflorescence, fruits initiated early have a lower probability of aborting than fruits initiated late.

These results suggest that low fruit set in *Yucca whipplei* is caused by shortage of resources to support developing fruits, rather than by a shortage of pollinators. Possible explanations of the adaptive significance of regulating maternal investment via fruit abortion are mentioned, but further experimentation is required before any conclusions can be drawn.

Introduction

Abortion of fruits is common in many plants (e.g., Stout 1927; von Steveninck 1957; Adams 1967; Luckwill 1970; Janzen 1971; Tomlinson and Soderholm 1975; Willson and Price 1977; Addicott 1978; Stephenson 1980). A number of adaptive roles for fruit abortion have been suggested, which may be categorized as follows:

(1) *Regulation of seed yield.* The number of offspring produced during a reproductive episode is an important component of the reproductive strategy of an organism (e.g., Cole 1954; Cody 1966; Williams 1966; Stearns 1976, 1977). For example, Lack (1947, 1954) recognized that many birds lay fewer eggs in a clutch than their physiological maximum and hypothesized that since siblings compete for limited resources, clutches of intermediate number yield the most offspring surviving to reproduce. Similarly, Salisbury (1942) and Johnson and Cook (1968)

have proposed that, for plants, the optimal number of seeds is the maximum number which can be provided adequate resources. To achieve the optimal number, plants must have the ability to control at least some of the components of seed yield (e.g., the number of flowers produced, the number of mature fruits per flower, the number of seeds per fruit) (Harper 1977; Primack 1978). By reducing fruit numbers fruit abortion may be an important component in regulating seed yield, matching fruit and seed numbers to the resources available to support their development (Salisbury 1942; van Steveninck 1957; Adams 1967; Janzen 1976; Willson and Price 1977; Lloyd 1980; Stephenson 1980).

(2) *Stress response.* Abortion of fruits may be a physiological response to severe environmental stress (e.g., Pawsey 1960; Janzen 1971) such as drought or frost, increasing the probability of survival of the plant by reducing its metabolic costs.

(3) *Selective elimination.* Abortion of fruits may be a mechanism for selectively eliminating fruits containing either (a) many aborted or unfertilized ovules, (b) seeds produced by selfing (Sweet 1973; Aker and Udovic 1981), (c) seeds which are otherwise genetically defective or inferior (Janzen 1977), or (d) seeds damaged by seed predators or pathogens (e.g., Janzen 1971). By eliminating these fruits, the plant may allocate more resources to other fruits, or to vegetative growth.

These hypotheses are not mutually exclusive. Indeed, if the abscission of a fruit is the result of an hormonal response to low rates of transmission of photosynthates, inorganic nutrients or water (Nitsch 1971; Addicott 1978), a synthetic view of fruit abortion and abscission emerges: a low rate of transmission of resources may be due either to characteristics of an individual fruit (such as low fertility, damaged or aborted seeds, or genetic "inferiority"), or to the physiological status of the plant (such as stress), or to competition between fruits for limited resources. Furthermore, the probability of abortion of inferior fruits, as well as the degree of physiological stress of the plant, may depend on the number of fruits initiating development and competing for nutrients.

Yucca whipplei (Agavaceae) occurs primarily in the chaparral and desert scrub communities of southern California and the Baja Peninsula. It produces a rosette which grows for a number of years, and then flowers once, producing a large, paniculate inflorescence. Some subspecies of *Yucca whipplei* reproduce clonally, producing clusters of rosettes (Haines 1941), but the subspecies which occurs at our two study sites (*Y. w. typica*) has a solitary rosette, and hence is monocarpic. An inflorescence may bear several thousand flowers, which open progressively from the bottom to the top of the panicle over a period of several

weeks. Flowers are pollinated by a moth, *Tegeticula maculata* (Prodoxidae), which lays its eggs in the ovaries of the flowers and then actively pollinates the same flowers (Riley 1892; Powell and Mackie 1966; Davis 1967; Aker and Udovic 1981). Although all flowers are hermaphroditic and hence ovuliferous, typically only about 10% of the flowers on an inflorescence produce mature fruits. Udovic (1981) has analyzed data on fruit set from a number of study sites and has shown that there is little variability, either within or between study sites, in the percentage of flowers which produce mature fruits.

In this paper we present evidence that the low fruit set of *Yucca whipplei* is the result of fruit abortion, and that fruit abortion is an important component in the regulation of seed yield. The role of fruit abortion in *Y. whipplei* in the elimination of inferior fruits or as a response to environmental stress remains to be determined.

Materials and Methods

During the spring of 1979, we marked a total of 108 flowering individuals at two sites (corresponding to CH3 and CH4; Udovic, 1981) at Pinyon Flat in the Santa Rosa Mountains (el. 1,200 m; Riverside County, California). Observations on the phenological status of each plant and the abundance and activity of pollinators were made at regular intervals throughout the flowering season (see Udovic, 1981, for a more detailed description).

We measured the basal area of the rosette as an index of the amount of resources (e.g., water, photosynthates) accumulated by the plant which could be allocated for reproduction. Since reproduction is concentrated in one episode, the stored reserves can be used most efficiently by shunting as much as possible to reproductive structures. For example, in *Agave deserti* a large fraction of the water and carbohydrates stored in the leaves of the rosette are mobilized to support the flowering process (Nobel 1977). Furthermore, in a long-lived monocarpic perennial such as *Yucca whipplei*, it is likely that a large fraction of the total resources spent on reproduction come from stored reserves rather than from resources obtained during the flowering season. Hence, there should be a strong positive correlation between stored reserves and actual reproductive expenditure. Indeed, at our sites, correlation coefficients for pairwise combinations of basal area of the rosette, maximal stalk height and the number of flowers produced are all highly significant ($p < 0.001$).

Several characteristics of floral and fruit development in *Yucca whipplei* facilitate counting of flowers and of aborted and maturing fruits. Artificial pollination experiments indicate that pollination of a flower almost invariably results in the initiation of development of a fruit, characterized by enlargement of the ovary and associated pedicel and a change in color from creamy white to green. By contrast, the ovary and pedicel on an unpollinated flower fail to enlarge, and the entire flower is eventually abscized. The pedicels remain on the branches of the panicle. During a brief period commencing at about the time a plant has completed flowering, small fruits may be abscized, sometimes in large numbers. Again, the pedicels of these fruits, which

are noticeably enlarged, remain attached to branches of the panicle. In early June, after all plants had stopped abscizing fruits, we obtained complete counts of the number of maturing fruits and the number of pedicels of both aborted (abscised) fruits and unfertilized flowers for each branch on each inflorescence. The vertical position of each branch relative to other branches on the panicle was also noted.

Results

At CH3, the mean number of flowers produced per inflorescence was $2,045 \pm 111$ (Table 1). On average, 79.3% of the flowers on an inflorescence failed to initiate fruits, 12.4% initiated fruits which were subsequently aborted, and 9.4% produced mature fruits. At CH4, on average, 82.5% of the $1,743 \pm 77$ flowers on an inflorescence failed to initiate fruits, 8.1% initiated fruits which subsequently aborted, and 9.4% produced mature fruits (Table 1). Fifty-one percent of all fruits initiating development were aborted and abscised.

If fruit abortion has a regulatory effect on fruit production, then the following relationships should result: (1) the proportion of fruits which abort should increase with the number of fruits initiated, and (2) the number of fruits which can be sustained by a plant should increase as the amount of resources available to support developing fruits increases. To test these predictions multiple regressions were obtained for the number of mature fruits produced (MF) and the number of fruits aborted (AF) as functions of the basal area of the rosette (BAR) and the number of fruits initiated (IF) for each study site. Analyses of covariance indicated no significant differences between sites in any of the estimated regression parameters; hence the data for the two sites were combined. If fruit abortion functions to reduce the number of fruits to a sustainable level, the expected relationship between variables will depend on whether fruit set is primarily limited by pollinators or by other resources. In order to restrict consideration to plants with adequate fertility, we have excluded from this analysis those 12 plants for which the percent of flowers initiating fruits was less than the mean percent of flowers producing mature fruits. We have also excluded 4 severely damaged inflorescences and 9 plants for which the reliability of counts of initiated fruits was uncertain, leaving a sample size of 85. Removal of plants with a low percentage of flowers initiating fruits yields a better fit because it eliminates one major source of nonlinearity, but does not affect the qualitative nature of the results.

The results (Table 2) demonstrate the following: (1) The partial regression coefficient for AF on IF (0.84) is significantly greater ($p < 0.001$) than the overall proportion of fruits which aborted (AF/IF = 0.51) in the population. Hence, the more fruits initiated by a plant, the greater the proportion of fruits aborted. (2) Nevertheless, even after adjusting for the effects of BAR

Table 1. Descriptive statistics (mean and standard errors) for characteristics of flowering individuals of *Yucca whipplei* at two study sites in the Santa Rosa Mountains

Site	#Plants	Basal area of rosette (BAR) (m²)	Stalk height (m)[a]	# Flowers[a]	# Initiated fruits (IF)[a, b]	# Mature fruits (MF)[a]	Mature fruits[a] per flowers
CH3	46	1.9 ± 0.1	3.24 ± 0.08	$2,045 \pm 111$	447 ± 49	194 ± 16	0.094 ± 0.005
CH4	62	1.5 ± 0.1	3.13 ± 0.07	$1,743 \pm 77$	305 ± 20	162 ± 10	0.094 ± 0.004

[a] Damaged plants at CH4 are not included in calculations
[b] Twelve plants (4 at CH3 and 9 at CH4) are not included in calculations because of difficulties in distinguishing pedicels of aborted fruits from those of unfertilized flowers

Table 2. Partial regression coefficients (and their 95% confidence intervals) for the number of aborted fruits (AF) and mature fruits (MF) as functions of the number of fruits initiated (IF) and the basal area of the rosette (BAR). r^2 is the proportion of the sum of squares explained by the multiple regression equations

Dependent variable	Independent variables	Partial regression coefficients	r^2
Aborted fruits (AF)	Basal area (BAR)	-55 ± 20	0.10
	Initiated fruits (IF)	0.84 ± 0.05	0.83
			0.93
Mature fruits (MF)	Basal area (BAR)	55 ± 20	0.43
	Initiated fruits (IF)	0.16 ± 0.05	0.17
			0.60

on both MF and IF, MF is an increasing function of IF ($p < 0.001$). This result indicates that fruit abortion is not a perfect regulator of mature fruit production (i.e., one which results in MF being totally independent of IF). (3) After adjusting for the effects of IF, AF is negatively correlated with BAR ($p < 0.001$), and MF is positively correlated with BAR ($p < 0.001$). Hence, given the same number of initiated fruits, large plants produce more mature fruits than small plants.

One further prediction of the regulation hypothesis emerges from the temporal flowering pattern of individual inflorescences. Flowers near the top of the inflorescence open later than flowers near the bottom. Hence fruits initiated near the bottom have a head start in development. If abortion is regulatory we expect that fruits initiated early will have a lower probability of abortion than those initiated late because they will have been initiated before the number of initiated fruits exceeds the number that the plant can support, and because once abortion does begin, those fruits to which the least resources have been committed are most likely to be aborted.

We compared the abortion rates for fruits in the upper $^1/_3$ of the inflorescence with abortion rates for fruits from the lower $^1/_3$, for ten infloresences. In all ten cases, abortion rates were higher for the upper $^1/_3$ and in six of the cases χ^2 values calculated from 2×2 contigency tables were statistically significant ($p < 0.005$). For the ten plants combined, 64.9% of the fruits initiated near the top of inflorescences aborted, while only 37.5% of the fruits initiated near the bottom aborted (Aker and Udovic 1981).

Discussion

These results, in conjunction with the high fruit abortion rate at our site (51%) lead us to conclude that most plants at our study site initiated more fruits than they could support, that larger plants could support more fruits, and that fruit abortion helped to reduce the number of fruits to a sustainable level. It is tempting to conclude that pollinators were not limiting. However, the number of mature fruits does increase slightly as a function of fertilized fruits, and the number of fertilized fruits is at least partly determined by pollinator availability. Furthermore, 12 of the 85 plants initiated fewer fruits than the mean number of fruits matured. Hence, it is likely that at least some of the plants in the population received an inadequate number of visits by pollinators. Nevertheless, our results, to-

gether with results on geographic variability in fruit set reported elsewhere (Udovic 1981) indicate that although pollinators are required for fruit initiation, the amount of resources available to support fruit development is considerably more important in determining the ultimate number of fruits matured.

An important evolutionary question emerges from these results: why does Yucca whipplei regulate maternal investment at such a late stage in the flowering and fruiting process? Lloyd (1979, 1980) has pointed out that there are three sequential stages at which regulation of maternal investment can take place in angiosperms: flower determination, ovary development, and fruit maturation. At which stages regulation occurs for a given species will depend on the nature of the selective regime, but, in general, regulation at an earlier stage reduces the amount of resources wasted in cancelled investments. The relative advantage of low-fruiting hermaphrodites, such as Yucca whipplei, which regulate at the fruit maturation stage, depends on the extent to which differences in the abilities of flowers to mature fruits are evident before anthesis. When the probability of pollination of individual flowers is uncertain or when the amount of resources available to support developing fruits is unpredictable, a low-fruiting hermaphrodite should have a selective advantage over plants which regulate maternal investment at earlier stages (e.g., andromonoecious plants which regulate ovary development, or hermaphrodites with high fruit set which regulate at the time of flower determination). This seems to be a plausible explanation for the reproductive behavior of Yucca whipplei, and it deserves further investigation. Pollinator availability varies temporally both within and between seasons. Plants which bloom either before or after the peak of pollinator abundance, or in a year of low pollinator abundance may increase the likelihood of receiving an adequate number of visits by pollinators if they produce more ovuliferous flowers than could support fruit.

Regulation at the fruit maturation stage provides the additional advantage of allowing for selective elimination of inferior fruits (Janzen 1977; Lloyd 1980). We currently have little direct evidence relating to the selective elimination hypothesis in Yucca whipplei. Preliminary findings indicate that abortion rates for selfed fruits are considerably higher than abortion rates for outcrossed fruits (Aker and Udovic 1981). However, in order to achieve a comprehensive view of the adaptive significance of fruit abortion in Yucca whipplei, further experimentation on the selective elimination hypothesis is required.

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