FLEXIBLE LIFE HISTORY TRAITS: SHIFTS BY SCARLET GILIA IN RESPONSE TO POLLINATOR ABUNDANCE[1]

KEN N. PAIGE[2] AND THOMAS G. WHITHAM
Department of Biological Sciences, Northern Arizona University,
Flagstaff, Arizona 86011 USA
and Biology Department, Museum of Northern Arizona, Flagstaff, Arizona 86001 USA

Abstract. In response to reduced levels of pollinators and pollination, scarlet gilia, *Ipomopsis aggregata,* shift from their normal semelparous mode of reproduction to iteroparous reproduction. When pollinators were excluded, plants were 5.5 times as likely to produce an ancillary rosette as controls that received natural pollinator levels. Similarly, when flowers were removed to prevent fruit production, experimental plants were 7.8 times as likely to produce an ancillary rosette as unmanipulated controls exposed to natural levels of pollination. Although ancillary rosette production is correlated with both season and a decline in pollinators, when seasonality was experimentally eliminated as a variable, changes in pollinator abundance still resulted in a corresponding change in rosette formation. Results suggest that there is a threshold below which an individual can be expected to switch from semelparity to iteroparity; the threshold appears to be between 30 and 40% fruit set. Our experiments also demonstrate a trade-off between cloning and fruit production at the population level.

Herbivory had no effect on these life history traits. Plants clipped to simulate natural herbivory by deer and elk showed no change in rosette formation relative to undamaged controls. These and other data demonstrate that pollinators are limiting and suggest that pollination is the primary factor involved in these life history trait shifts by scarlet gilia. Midseason shifts in life history traits permit plants to adjust to current lows in pollinator services by producing an ancillary rosette that can then flower in a subsequent year when pollinators may be less limiting.

Key words: ancillary rosette; cloning; Hyles lineata; Ipomopsis aggregata; *iteroparity; life history trait shifts; pollinator abundance; reproductive success; scarlet gilia;* Selasphorus platycercus; Selasphorus rufus; *semelparity.*

INTRODUCTION

The ability of an organism to respond differentially to changing conditions is crucial to its short- and long-term survival. Because plant life history traits are often viewed as fixed, phenotypic plasticity in response to changing conditions is not expected. In contrast to other ecological factors (Harper and Ogden 1970, Abrahamson 1975, Werner and Platt 1976, Charnov and Bull 1977, Hartnett and Abrahamson 1979, Doust and Cavers 1982, Marshall et al. 1985, Whitham and Mopper 1985) few ecologists have examined how pollinators might affect the life history traits of individual plants (Bierzychudek 1981). An earlier study of scarlet gilia, *Ipomopsis aggregata,* demonstrated that individual plants shift the color (Paige and Whitham 1985) and nectar secretion patterns (K. N. Paige, *personal observation*) of their flowers to take advantage of changing pollinator species during the flowering season. Here we show that in addition to changes in floral traits, *I.*

aggregata can also shift from its normal semelparous mode of reproduction to iteroparous reproduction; a response to low levels of fruit set and ultimately a consequence of pollinator abundance.

Ipomopsis aggregata is ideally suited for studying life history traits because it is facultatively iteroparous. Although *I. aggregata* is considered to be semelparous or monocarpic (e.g., Hainsworth et al. 1985), i.e., the plant dies after flowering, in Arizona we observed some individuals that were iteroparous or polycarpic. These latter individuals produced an ancillary rosette at the base of the flowering stalk. Thus, even though the flowering rosette dies after blooming, the ancillary rosette survives to flower in a subsequent year.

By examining this facultative shift in life history, this paper addresses the following questions: (1) What are the normal patterns of semelparous and iteroparous reproduction in scarlet gilia? (2) With the removal of pollinators can a semelparous plant be induced to shift to an iteroparous mode of reproduction? (3) Does seasonality influence a plant's pathway of reproduction? (4) Do herbivores influence these life history traits? (5) Is there a trade-off between the level of sexual reproduction and cloning, and if so, what is the relationship?

METHODS

The relationship between fruit set and ancillary rosette production was studied from 1983 through 1985 on Fern Mountain (elevation 2500 m), near Flagstaff, Arizona. Pollinator densities were censused during standardized walks at ≈3-d intervals throughout the flowering season. Pollinators included the Broad-tailed Hummingbird (*Selasphorus platycercus*), the Rufous Hummingbird (*S. rufus*), and a single species of hawk-moth, the white-lined sphinx (*Hyles lineata*).

Over 1200 individually tagged plants were censused along a transect to determine the relative frequencies of semelparous vs. iteroparous individuals at different times during the flowering season. Although the flowering season lasts 2¼ mo, individuals flower for ≈3 wk. Thus, to examine the frequency of iteroparity as a function of flowering time, plants were seasonally divided into early-, middle-, and late-flowering individuals.

To determine the relationship between pollinator abundance and fruit set, fruit set was recorded for each of the three census periods. Because fruit set and seed set are correlated ($r^2 = 88.7$, $n = 10$, $P < .001$, $y = 9.84 + 0.0733x$ [±0.0092, standard error of the slope]), discussion will be restricted to fruit set (Scarlet gilia produces an average of 7.2 ± 0.39 seeds per fruit, $n = 110$).

To examine the effect of fruit set on ancillary rosette production, two experiments were conducted. Early in the season, prior to flowering, 26 individual plants were randomly selected and covered with nylon-tricot–covered wire cages to exclude pollinators. At the same time, flowers and buds were removed from 23 randomly selected individuals to prohibit the plants from setting fruit. Plants were periodically checked and new buds or flowers were removed. As a control, 21 plants were randomly selected and exposed to natural levels of pollination. At the end of the flowering season, these plants were examined for the presence of ancillary rosettes.

To quantify the effects of herbivory on cloning, the inflorescences of 30 flowering plants were experimentally clipped, removing up to 95% of the aboveground biomass, to simulate natural herbivory (mule deer and elk eat inflorescences, never flowers alone). Twenty-one undamaged, unmanipulated plants served as a control. At the end of the flowering season these plants were checked for the production of ancillary rosettes.

To determine whether fruit set was limited by energy or pollinator availability late in the season, 20 plants were hand-pollinated and compared with 12 naturally pollinated individuals.

RESULTS

Observational data

To examine the mechanisms responsible for why some plants are semelparous and others iteroparous,

FIG. 1. Illustration of scarlet gilia comparing clonal and nonclonal individuals. Cloning can be characterized by the production of a new leafy basal rosette.

we first present data to illustrate patterns of pollinator abundance, fruit set, and cloning.

Some plants died after flowering, but in others a rosette developed as the flower stalk and basal leaves died back (Fig. 1). Of 343 plants that both flowered and produced rosettes in 1983, all rosettes were alive in 1984 and 10% flowered. Because no significant differences were found in the levels of cloning between the different color variants of *Ipomopsis* ($\chi^2 = 2.26$, df = 4, $P > .25$), plants of different flower colors were grouped for further analyses.

Plants that flowered early in the season were likely to be semelparous, while those that flowered late were likely to be iteroparous. Only 18% of all individuals that initiated flowering on or near 15 July produced ancillary rosettes, compared with 53% of all individuals that began flowering on 25 August ($\chi^2 = 102.74$, df = 2, $P < .001$; Table 1).

TABLE 1. Percentage of scarlet gilia that produced ancillary basal rosettes on three separate dates in 1983 in relation to the level of pollination (as indicated by fruit set). Number of observations in parentheses.

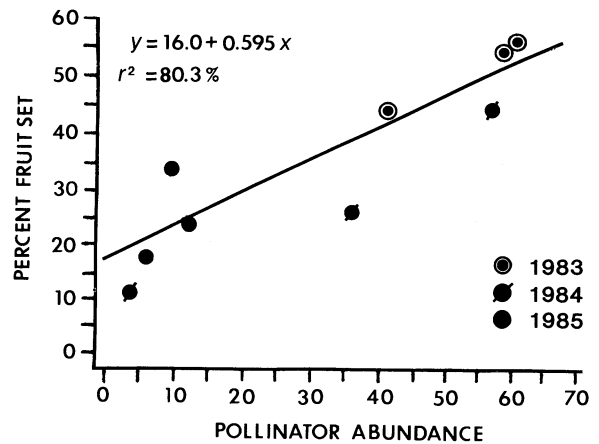|	Date of flowering initiation		
	15 July	3 August	25 August
Cloning	18 (397)	23 (629)	53 (237)
Fruit set	57 (22)	55 (17)	43 (23)

FIG. 2. Correlation between the level of fruit set and pollinator abundance. As the number of pollinators increases, the level of fruit set increases. Data are based on early-, middle-, and late-flowering plants over 3 yr, 1983–1985. Standard error of the slope = ±0.1040. Hummingbirds decreased in number from an average of 26 individuals early in the season to 0 late in the season in 1983, from 36 to 0 in 1984, and from 5 to 0 in 1985.

Associated with the seasonal increase in cloning was a decline in fruit set. Fruit set in the 15 July cohort (57%) was significantly higher than fruit set in the 25 August cohort (43% on average, ANOVA: $F = 3.21$; df $= 2,59$; LSD multiple range test, $P < .05$; Table 1).

The seasonal changes in fruit set and cloning were strongly correlated with pollinator abundance. Over a 3-yr period, each year, mean pollinator abundance was recorded for early-, middle-, and late-flowering plants. Each year, the number of pollinators dropped by an average $59 \pm 18.8\%$ from early to late in the season (from 43 to 17 pollinators on average; $\chi^2 = 21.15$, df $= 4$, $P < .05$). The seasonal decline in pollinator abundance is largely due to changes in hummingbird abundance; their populations remain stable through July, then steadily decline through August until none remain by early September (on average $84 \pm 8.9\%$ of the decline in pollinator number can be attributed to the loss of hummingbirds). When hummingbirds emigrate, hawkmoths become the sole pollinators, and their abundances remain stable to the end of the flowering season (Paige and Whitham 1985). As hummingbirds declined, the percentage of flowers that developed into fruits also declined (Fig. 2; $r^2 = 80.3\%$, $n = 9$, $P < .05$). For example, as pollinator abundance decreased from 60 to 5 pollinators within the census areas of ≈ 5 ha, the percentage of flowers that developed into fruits decreased from 55 to 20%. Therefore, fruit set and pollinator abundance were positively correlated. It is also important to note that fruit set is primarily a result of interplant pollen transfer and not a result of self-pollination or apomixis (Paige and Whitham 1985).

Fruit set is ultimately limited, not by energy levels, but by pollinator activity. Plants in which all flowers were hand-pollinated late in the season set a significantly higher percentage of fruit than control plants exposed to natural levels of pollination ($53 \pm 7.9\%$ vs. $34 \pm 4.4\%$, $t = 2.07$, df $= 30$, $P < .05$).

When hummingbirds were experimentally excluded, fruit set declined. Experimental plants exposed only to hawkmoths set an average of 32% fruit, whereas plants exposed to both hawkmoths and hummingbirds set 46% fruit (in Paige and Whitham 1985; hummingbirds were excluded by covering plants with nylon-tricot–covered wire cages during the day). These results reflected natural conditions (see Table 1). Plants from which hummingbirds were experimentally excluded set 30% less fruit than plants exposed to both pollinators, while under natural conditions plants set 25% less fruit with the loss of hummingbirds ($\chi^2 = 0.64$, df $= 1$, $P > .25$; both natural and experimental results are from the 1983 field season).

With declining pollinator services and a subsequent decline in the number of flowers setting fruit, individual plants were far more likely to produce ancillary rosettes. As fruit set declined from 100 to 0%, the probability of being iteroparous increased from 0 to 100%. Thus, fruit set and cloning are inversely related ($r^2 = 79.4\%$, $n = 11$, $P < .05$; Fig. 3). On average, iteroparous individuals set $36.7 \pm 4.0\%$ fruits, whereas semelparous plants set $57.7 \pm 2.7\%$ fruits ($t = 4.25$, df $= 74$, $P < .001$).

Experimental data

To show that pollinators are ultimately responsible for the observed shift to iteroparity, we performed two experiments that separated cause and effect and eliminated an alternative hypothesis of seasonally induced shifts in cloning.

First, plants that were caged early in the growing season to exclude pollinators were 5.5 times as likely to clone as uncaged control plants (27 vs. 5%, respectively; $\chi^2 = 4.03$, df $= 1$, $P < .05$). Second, plants whose buds were removed to eliminate fruit set were 7.8 times as likely to clone as controls exposed to natural levels of pollination ($\chi^2 = 7.37$, df $= 1$, $P < .05$, 39 vs. 5%).

These experiments also demonstrate that independent of season, pollinators alone can trigger the switch
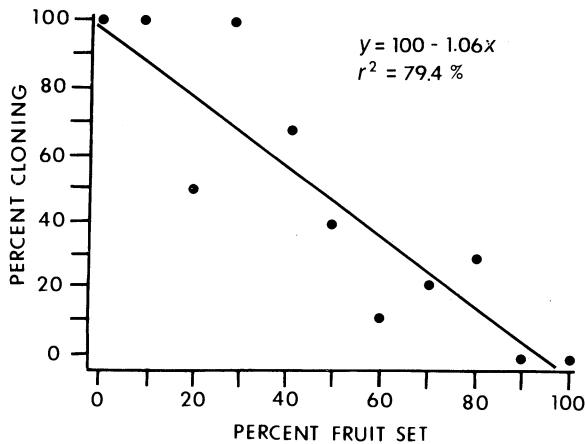
$$y = 100 - 1.06x$$
$$r^2 = 79.4\ \%$$

FIG. 3. Correlation between the level of fruit set and the level of cloning for scarlet gilia. As fruit set increases, clone production declines. Data are based on 76 plants, each randomly selected from one of the three census dates of the 1983 flowering season. Plants were categorized according to the percentage fruit set (i.e., the percentage plants cloning that set 0% fruit, 1–10% fruit, 11–20% fruit, etc.). Standard error of the slope = ±0.1799.

from semelparity to iteroparity. Although the correlative studies of Table 1 and Figs. 2 and 3 showed that iteroparity was correlated with both season and a decline in pollinators, in the above experiments both experimental and control groups were initiated at the same time. Thus, in these experiments cloning occurred independently of seasonal influences.

Simulated herbivory had no effect on rosette formation. Rosette formation by plants that had up to 95% of their aboveground biomass removed (to simulate natural herbivory by deer and elk) and by undamaged plants were not significantly different ($\chi^2 = 0.078$, df = 1, $P > .25$; see Paige and Whitham 1987).

Furthermore, no significant seasonal differences in temperature or precipitation were detected that might account for the production of rosettes. During the three major census periods of this study temperature and precipitation did not significantly change (ANOVA: $F = 3.03$, df = 2,59, $P > .06$ and $F = 1.00$, df = 2,59, $P > .10$, respectively; comparisons were made between the three sampling dates: 15 July, 3 August, and 25 August) and were therefore uncorrelated with the seasonal decline in fruit set and corresponding increase in rosette production.

DISCUSSION

Experimental manipulations show that the flexible life history traits of scarlet gilia represent an adaptive response to changes in pollinator abundance. In response to low fruit set, individual plants are able to reallocate resources to rosette formation, thereby shifting from semelparity to iteroparity; the subsequent flowering of an ancillary rosette offers another chance at seed production.

Our results are unique for two reasons. First, we have demonstrated that individuals of a species generally thought to be semelparous can become iteroparous. Second, we have experimentally identified the biological factor responsible for the shift: pollinator abundance.

Our results suggest that there may be a threshold below which an individual can be expected to switch from semelparity to iteroparity. In the field, 77% of all individuals setting 36% (average fruit set for individuals that cloned) or less fruit produced an ancillary rosette, whereas only 24% of all plants that set >36% fruit produced an ancillary rosette. Thus the threshold appears to be between 30 and 40%.

Our experiments also demonstrate that there is a trade-off between cloning and fruit production at the population level. Because the relationships between pollinator abundance and fruit set and between fruit set and cloning are strongly correlated (Figs. 2 and 3), we can predict the impact of changing pollinator densities on life history traits. Using the regression equations from Figs. 2 and 3, for every additional pollinator on our study site, fruit set increased by 0.55%, while cloning decreased by 0.59%. Consequently, at the population level, these data suggest that there is a one-to-one trade-off between the percent fruit set and the percent cloning (i.e., the switch from semelparity to iteroparity).

Although pollinators have probably played an important role in the evolution of certain plant life history traits, supportive evidence has been indirect (Schaffer and Gadgil 1975, Schaffer and Schaffer 1977, 1979, Silvertown 1982:82–108). Our results show that pollinators can directly affect the life history of a plant and that individuals can behave plastically in response to the level of pollination (as measured by fruit set). Our results were not explained by the effects of seasonality or herbivory.

In contrast to the plants at Fern Mountain, which typically switch to iteroparity as a function of pollinator abundance, *Ipomopsis aggregata* rarely clones and is almost exclusively semelparous at lower elevations where pollinator densities do not decrease (of 310 plants censused at low elevation [2100 m] only 0.3% of all individuals were found cloning late in the season). Of 37 plants that were caged at low elevation to exclude pollinators, only one produced an ancillary rosette. This suggests that flexibility in life history traits may represent a local adaptation reflecting the loyalty or predictability of pollinators at a specific site (e.g., see Paige and Whitham 1985). Whether the observed switching behavior by these plants at higher elevations is genetically based remains to be determined.

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