Reproduction and life history theory in semelparous and iteroparous varieties of yucca whipplei

Travis Eugene Huxman
REPRODUCTION AND LIFE HISTORY THEORY IN SEMELPAROUS AND ITEROPAROUS VARIETIES OF YUCCA WHIPPLEI

A Thesis
Presented to the
Faculty of
California State University,
San Bernardino

In Partial Fulfillment
of the Requirements for the Degree
Master of Science
in
Biology

by
Travis Eugene Huxman

June 1996
REPRODUCTION AND LIFE HISTORY THEORY IN SEMELPAROUS AND ITEROPAROUS VARIETIES OF YUCCA WHIPPLEI

A Thesis
Presented to the Faculty of California State University, San Bernardino

by Travis Eugene Huxman
June 1996

Approved by:

Michael E. Loik, Biology, Committee Chair

David M. Polcyn, Biology

James A. Ferrari, Biology

James des Lauriers, Life Science, Chaffey College

June 10, 1996 Date
ABSTRACT

Characteristics of flowering *Yucca whipplei* were evaluated for two varieties exhibiting significantly different reproductive strategies. Differences in reproduction for two varieties of *Yucca whipplei* were investigated to assess trade-offs in reproduction associated with different life history strategies. Flower, fruit and seed production, and reproductive expenditure were compared for *Yucca whipplei* var. *whipplei*, a semelparous plant and *Yucca whipplei* var. *caespitosa*, an iteroparous plant. Leaf surface area, leaf area index, inflorescence size, total flowers, total mature fruit, total seed production and seed viability were determined for 40 individual plants for each variety. There were no significant differences in leaf surface area for the two varieties, however, the number of viable seeds produced per leaf surface area by *Y. w.* var. *whipplei* was greater than for *Y. w.* var. *caespitosa*. There was a significant difference in germination rates and percent germination between the two varieties; variety *whipplei* had greater seed viability than did var. *caespitosa*. The total number of viable seeds per plant increased with inflorescence size for var. *caespitosa* but at a lower rate than for var. *whipplei*. The percentage of viable seeds per plant showed a negative relationship to inflorescence size for var. *whipplei*. There was no such relationship for var. *caespitosa* suggesting that attached rosettes could provide some resources for the production of viable seeds. The flower, fruit, and seed production data was subjected to evaluation with the reproductive effort model of the evolution of semelparity. The semelparous var. *whipplei* did not fit the predictions of the model, describing the of evolution semelparity in *Y. whipplei*. Fire and other disturbances
may have led to the evolution of semelparity. The results indicate that *Yucca whipplei* var. *whipplei* concentrates its resources on one episode of reproduction that results in greater numbers of high-quality seed compared to *Yucca whipplei* var. *caespitosa*. 
ACKNOWLEDGMENTS

I would like to express my appreciation to the members of my thesis committee, Michael Loik, David Polcyn, James Ferarri, and James des Lauriers for their support and interest in the development of this project. Without their help and critique, this project would not have been possible. In addition, I would like to extend my appreciation to the faculty of the Department of Biology and a core of graduate students who provided an atmosphere in which research was important for a developing student.

I would not have had the ability to complete this thesis if it were not for the support of my wife Kim. I cannot express in words the appreciation I feel towards her and the way she helped me to complete this degree. Whether it was help in the field, lab or home, she provided me with the time and energy I needed to finish this project. In addition, I want to thank my family, Ron, Nancy, Jake, Al and Dot for the help they provided throughout my education. I would also like to thank Marc Stamer for the time he spend getting stabbed by yuccas, and the conversations that led to the questions addressed in this thesis.
# TABLE OF CONTENTS

ABSTRACT ............................................................... iii

ACKNOWLEDGMENTS ..................................................... v

LIST OF TABLES ....................................................... vii

LIST OF FIGURES ...................................................... viii

CHAPTER ONE

*Yucca whipplei* and life history theory ........................................... 1

CHAPTER TWO

Life history trade-offs in reproduction for two varieties of *Yucca whipplei* (Liliaceae) .................................................. 10

Materials and Methods ................................................. 12

Results ................................................................. 15

Discussion ............................................................ 19

CHAPTER THREE

The reproductive effort model and evolution of semelparity in *Yucca whipplei* ................................................................. 25

Materials and Methods ................................................. 28

Results ................................................................. 30

Discussion ............................................................ 32

CHAPTER FOUR

Summary ................................................................. 36

LITERATURE CITED .................................................... 54
Table 2.1. Relationships between leaf length and area, inflorescence height and diameter, as well as number of seeds and fruit size for both varieties of Yucca whipplei. N = 50 for leaf surface area to leaf length, N = 20 for inflorescence height to diameter at base, N = 30 for number of seeds per fruit to length of fruit. 40

Table 2.2. Vegetative and floral characteristics for Yucca whipplei var. whipplei and Yucca whipplei var. caespitosa. Data are means ± 1 SE, N = 40 plants. Means for Yucca whipplei var. caespitosa are from one reproductive event and all attached rosettes. 41

Table 2.3. Reproductive efficiency for the two varieties of Yucca whipplei. Data are means ± 1 SE. Means from Yucca whipplei var. caespitosa are from multiple attached rosettes. LSA is leaf surface area. N = 40. 42

Table 3.1. Fecundity per unit reproductive effort for both varieties of Yucca whipplei measured in the field. Data are expressed as means ± one SE. N = 40. 43
Figure 2.1. The percent of seeds that germinated for Yucca whipplei var. whipplei (●) and Yucca whipplei var. caespitosa (■). Seeds were placed on wet filter paper in Petri dishes for over twenty days. Data are means ± SE, N = 40 plants for each variety.

Figure 2.2. Seed viability as a function of inflorescence size for Yucca whipplei var. whipplei. (Seed viability) = -47 (Inflorescence height) + 282, N = 40, \( r^2 = 0.52, P < 0.05 \).

Figure 2.3. The number of viable seeds produced by individuals of Yucca whipplei var. whipplei as a function of leaf surface area (LSA). (Viable seeds) = \(-23(LSA)^2 + 1606(LSA) - 1264\), N = 40, \( r^2 = 0.51, P < 0.05 \).

Figure 2.4. The number of viable seeds produced by individuals of Yucca whipplei var. caespitosa as a function of the total number of rosettes.

Figure 3.1. The fruit to flower ratio (a measurement of fecundity per unit reproductive effort) plotted against inflorescence height (reproductive effort) for (A) Yucca whipplei var. whipplei (●) \( r^2 = 0.09 \) and (B) Yucca whipplei var. caespitosa (■) \( r^2 = 0.03 \).

Figure 3.2. The number of viable seeds per flower as a function of the inflorescence height of (A) Yucca whipplei var. whipplei (●) \( r^2 = 0.16 \) and (B) Yucca whipplei var. caespitosa (■). \( r^2 = 0.02 \).

Figure 3.3. The relationship between viable seeds per leaf surface area (m2) and inflorescence height for (A) Yucca whipplei var. whipplei (●) \( r^2 = 0.33, P < 0.05 \) and (B) Yucca whipplei var. caespitosa (■). \( r^2 = 0.07 \).

Figure 3.4. The relationship between the number of fruit per leaf surface area and leaf surface area for (A) Yucca whipplei var. whipplei (●) \( r^2 = 0.06 \) and (B) Yucca whipplei var. caespitosa (■). \( r^2 = 0.26 \).

Figure 3.5. The relationship between the number of viable seeds per leaf surface area and the leaf surface area of (A) Yucca whipplei var. whipplei (●) \( r^2 = 0.59, P < 0.05 \) and (B) Yucca whipplei var. caespitosa (■). \( r^2 = 0.24 \).

Figure 3.6. The relationship between the number of seeds per leaf surface area and leaf area index of (A) Yucca whipplei var. whipplei (●) \( r^2 = 0.65, P < 0.01 \) and (B) Yucca whipplei var. caespitosa (■). \( r^2 = 0.05 \).
Terrestrial plants display an extreme amount of life history variation with respect to strategies of reproduction. The environment dictates life history strategy and physiological and morphological characteristics that result in patterns of reproduction whose strategies will be advantageous under certain pressures in specific ecosystems. In order to maximize overall fitness, an organism should balance the costs and benefits of current reproduction in comparison to its long term future prospects (Williams, 1966). An individual with an increased probability of future reproductive success would be less likely to risk resources in present reproductive activities than another individual with a reduced probability of future success (Pianka, 1988). These concepts shape the characteristics of individual plant reproductive strategy with respect to the investment in propagules an individual produces in any one reproductive event, with current investment in reproduction inversely related to the probability of successful future reproductive events (Pianka, 1988). Small relative investments are typical in perennial plants that reproduce over multiple seasons as compared to the relatively large investment made by an annual which only reproduces once. When a perennial life history strategy does not produce the quantity of seeds over a life time that an annual life history strategy produces for the same individual in the same conditions, the annual strategy is favored (Charnov and Schaffer,
1973). A shift in life history strategy from perennial to annual reproduction is associated with an increase in the chance of senescence of the reproducing individual.

Semelparity is the life history phenomenon in which a single massive episode of reproduction is followed by rapid degeneration and death of the reproductive individual (Schaffer and Schaffer, 1977). Iteroparous individuals produce offspring over several reproductive events and spend energy on post-flowering survival (Schaffer, 1974a). Long lived semelparous plants are rarely abundant in an ecosystem, but are geographically widespread and taxonomically common (Ricklefs, 1990; Young and Augspurger, 1991). There is some difficulty comparing long lived semelparous plants to the characteristics of typical $r$ selected species (Pianka, 1970). Typical $r$ selected individuals would be expected to have rapid development, high intrinsic rates of increase, early (time from establishment to first reproductive event) reproduction and small highly mobile seeds (Pianka, 1970). Long lived semelparous plants have more characteristics in common with $K$ selected species that exhibit slow development, delayed reproduction, large size, and a longer life span, but long lived semelparous plants have a single reproductive event. Because long lived semelparous plants exhibit unique patterns of reproduction, extensive modeling has taken place to explain their evolution (Young, 1990; Young and Augspurger, 1991).

Life history models have often addressed adaptations as “optimal” strategies. The theory of optimal reproductive strategies was developed to examine trade-offs between current reproduction, future survival and future reproductive success that plants face in balancing use of finite resource storages. Different selective pressures apparently exist which may have produced the semelparous reproductive strategy. The theory of optimal
reproductive strategies suggests that there is a trade off between: 1) energy placed into current fecundity, 2) energy available for post-flowering survival and 3) subsequent reproductive value of individuals (Williams, 1966; Schaffer, 1974a). Reproductive value is the expected output (i.e. seeds) of an individual at a particular age relative to a newly established individual (Schaffer 1974b; Ricklefs, 1990). When post-flowering survival is low or uncertain, and current reproductive value is higher than subsequent reproductive value, current fecundity is high. This can lead to selection favoring semelparous reproduction (Schaffer, 1977). If the relationship between initial reproductive value and post-flowering reproductive value increases, selection favors an iteroparous reproductive strategy. The optimal reproductive strategies theory suggests that there are relationships between fecundity and reproductive effort (the amount of resources used to produce a particular level of fecundity). These functional relationships change with life history reproductive strategy. More specifically, the theory suggests that when selection favors an increase in fecundity per unit reproductive effort with increases in reproductive effort, semelparity will be favored; “the reproductive effort model” (Schaffer and Schaffer, 1977 and 1979; Young and Augspurger, 1991).

The reproductive effort model predicts three situations in which the selection for a larger seed crop in a single reproductive event (semelparity) is favored through a positive correlation between fecundity per unit effort and reproductive effort (Schaffer and Schaffer, 1977 and 1979; Rathcke and Lacey, 1985; Young and Augspurger, 1991). First, the seeds of small inflorescences are heavily preyed upon while larger inflorescences produce sufficient numbers of seeds to overwhelm seed predators (Rathcke and Lacey,
If larger inflorescences lead to an increase in the percentage of seed set under such conditions, the semelparous strategy would be favored. This relies on the assumption that inflorescence size determines the number of seeds produced and that iteroparous reproduction entails small inflorescences. Reaction to this type of pressure can shape individual and community reproductive habit in ways that do not involve semelparity, as in the case of mass synchronized reproduction by bamboos (Janzen, 1976), and masting by the southwest riparian walnut, *Juglans major* (Stromberg and Patten, 1990).

In the second strategy, pollinators would preferably forage on the largest inflorescences available because large inflorescences have a large number of flowers, and therefore, greater rewards (Schaffer and Schaffer, 1977; Udovic, 1981). The benefit to a pollinator’s energy budget are significant enough to outweigh the cost of foraging in a non-random manner. When the number of pollinators relative to the number of flowers is small, differential selection occurs between small and large inflorescences with respect to pollination of flowers, in that instance, large inflorescences would be favored, reducing post flowering survival and subsequent reproductive values, ultimately leading to the semelparous reproductive habit (Schaffer and Schaffer, 1977 and 1979).

In the third strategy, under resource limited conditions, fecundity per unit reproductive effort is positively correlated with reproductive effort due to the risk involved in flowering under unpredictable conditions (Schaffer and Gadgil, 1975). Reproductive effort is defined here as the resources allocated by the plant to reproduction. As reproductive effort increases, post-flowering survival decreases. Because of the risks involved in flowering when resources are unavailable, future adult survival is uncertain,
and a single reproductive event could produce more offspring than multiple events, maximizing fecundity (Schaffer, 1974b). For example, the water that a semelparous Agave sp. may expend during a flowering event will not be replaced for an extended period of time (Schaffer and Schaffer 1977). The loss of water, even in a small reproductive event, may be sufficient to cause the demise of the individual. Populations of semelparous Yucca whipplei vary in the number of individuals that flower between optimal and poor years due to lack of resources in poor years. Iteroparous Yucca sp. have a specific root morphology that allows them access to groundwater, whereas semelparous Yucca whipplei and Agave sp. have a shallower root system that takes up water near the soil surface following rainfall. Iteroparous plants apparently have access to a constant resource supply whereas the semelparous individuals do not, thus the availability of resources is much more predictable and residual reproductive value is increased enough to favor iteroparity.

**Yucca whipplei**

Reproductive strategies vary within the genus *Yucca* in North America, with a single species being semelparous while the remainder are iteroparous (Schaffer and Schaffer, 1979; Udovic, 1981; Aker, 1982b). Semelparous reproduction in *Yucca* and *Agave* is characterized by the post-flowering half life, which is the length of time after flowering for half of the population to die, usually around 3 months for *Yucca* and *Agave* (Schaffer and Schaffer, 1977 and 1979). The presence of semelparous reproduction does not reflect phylogenetic patterns within the genera *Yucca* and *Agave* (i.e. it has apparently
evolved independently in several taxonomic groups), nor does this type of reproduction reflect the phylogeny of the pollinator groups as Yucca and Agave have specific individual insect species which exclusively pollinate plants (Schaffer and Schaffer 1977). The conditions which give rise to semelparous reproduction are critical for understanding life history theory, because semelparity is ecologically and taxonomically widespread (Young and Augspurger, 1991).

Yucca whipplei (Liliaceae) Torrey. is a monocarpic perennial that is distributed from the San Diego coast east and north into the Great Basin (Haines, 1941; Aker, 1982a). Schaffer and Schaffer (1977) have classified this species of yucca as being semelparous due to the extremely low post-flowering half life exhibited by several populations. There is considerable variation in morphology and life history strategy for Y. whipplei, with up to five subspecies or varieties being recognized depending on taxonomic reference (Wimber, 1958; Hickman, 1992). Two of the subspecies are truly monocarpic (semelparous), whereas three are iteroparous (Haines, 1941; Wimber, 1958). Within the San Bernardino basin, Yucca whipplei var. whipplei and Yucca whipplei var. caespitosa overlap in distribution (Haines, 1941).

Yucca whipplei produces a large floral display after several years of vegetative growth (Haines, 1941). The inflorescence ranges in height from two to four meters depending on the variety (Haines, 1941). The single panicle contains between one hundred and several thousand hermaphroditic flowers, which open progressively from the bottom to the top of the inflorescence (Aker, 1982a). The inflorescence is visited primarily by the moth pollinator, Tegeticula maculata (Wilder, 1964; Udovic, 1981). A
significant difference exists between the number of flowers pollinated and the number of fruit which are maintained by the inflorescence, and variation in the ratio of matured fruit to the number of flowers produced appears to be correlated with inflorescence size (Udovic, 1981). Specific germination requirements for seeds and conditions for seedling establishment differ among the varieties. *Yucca whipplei* exhibits within-fruit seed germination of seeds which may enhance seedling establishment (Huxman and Loik, 1996b).

Schaffer and Schaffer (1977) originally hypothesized that the optimal foraging behavior exhibited by the pollinator of *Yucca whipplei* was the agent responsible for selection of semelparity. This was determined by comparing the ratio of fruit maturing on the inflorescence to the number of flowers reaching anthesis as a function of different size classes of inflorescence. They showed an increase in fruit number with an increase in inflorescence size (Schaffer and Schaffer, 1977). Subsequent research found conflicting measurements and attributed the difference to sample size and original assumptions about the number of flowers actually pollinated (Aker, 1982a). Schaffer and Schaffer (1977) did not test the remaining two hypotheses of optimal reproductive strategies; they discounted predation pressure by the lack of evidence within the literature and the numerous field observations they had made. Udovic and Aker (1981) showed that the yucca pollinator was indeed limiting and appeared to limit seed production, but the number of fruit on the inflorescence was always less than the number of flowers pollinated. This suggests that the selection for a large floral display and semelparity does not come as a result of the
specific foraging behavior of the pollinator, but may be due to other factors such as resource limitation (Udovic and Aker, 1981; Aker, 1982a and 1982b).

*Yucca whipplei* has been shown to regulate plant reproductive expenditure at the flowering and fruiting stages of reproduction (Aker, 1982). The ratio of matured fruit to the total number of flowers reaching anthesis, along with the amount of resources that are used for flowering, are used as a measure of the semelparity of the organism (Schaffer and Schaffer, 1977 and 1979; Udovic, 1981; Aker, 1982). Specifically, the fruit to flower ratio and the plant’s basal area (shaded ground of the plant) are indicators of the seed crop and reproductive effort, respectively. Since reproduction requires the majority of translocatable resources available in yuccas, the amount of such resources has been used to determine the total cost of flowering (Udovic and Aker, 1981).

The major limiting factor for flowering of desert succulents is the availability of sufficient water (Nobel, 1977). For *Yucca whipplei* var. *caespitosa* attached rosettes may translocate resources to flowering stems. In *Agave deserti* adjacent connected stems undergo water stress when the central rosette flowers, and shunting of water and carbon between ramets is common (Nobel, 1977; Tissue and Nobel, 1990a and 1990b). Resource translocation between rosettes may allow *Y. whipplei* var. *caespitosa* to overcome resource limitation. The iteroparous variety may be lowering the resource limitations compared to the semelparous *Yucca whipplei* var. *whipplei*.

There is anecdotal evidence to support the idea that limited resources have selected for increased reproductive effort in *Yucca whipplei*. Re-examination of *Yucca whipplei* with the reproductive effort model, including a greater sample size, as well as a
variety of measurements of reproductive effort and fecundity would allow for the implications of limiting resources to be assessed. In this case, there is a need for examination of phenology of the semelparous *Y. w.* var. *whipplei* and the iteroparous *Y. w.* var. *caespitosa*. This species, with variation between varieties with respect to life history strategy, provides an excellent system for testing population models that attempt to explain semelparity.
Reproductive strategies vary within the genus *Yucca*, with some species being semelparous whereas others are iteroparous (Schaffer and Schaffer, 1979; Udovic, 1981; Aker, 1982a). Semelparity is the life history phenomenon whereby resources are spent on a single episode of reproduction that is followed by rapid degeneration and death of the reproductive individual (Schaffer and Schaffer, 1977); iteroparous individuals exhibit several reproductive events and spend some of their resources to ensure post-flowering survival (Schaffer, 1974a). Semelparous reproduction in yuccas can be characterized by the post-flowering half-life and by measurements of reproductive expenditure and efficiency (Schaffer and Schaffer, 1977 and 1979). Semelparous reproduction does not follow specific phylogenetic patterns within yuccas or agaves (i.e. it has apparently evolved independently in several taxonomic groups), nor does this strategy reflect the phylogeny of the pollinator groups (Schaffer and Schaffer, 1977). The conditions that give rise to semelparous reproduction are critical to understanding life history theory, because semelparity is ecologically and taxonomically widespread (Young, 1990). Seed production and seed viability in closely related varieties of many species have not yet been investigated in terms of life history theory (Aker, 1982b).
Yucca whipplei (Liliaceae) Torrey is a perennial rosette that is distributed from
the Pacific coast near San Diego north into the Mojave Desert of southern California
(Haines, 1941; Aker, 1982a). Schaffer and Schaffer (1977) have classified this species of
yucca as being semelparous because of the extremely low post-flowering half life observed
for several populations. This is the sole yucca species that is considered semelparous,
even though several varieties have an iteroparous life history strategy. There is
considerable variation in growth form for Y. whipplei, with up to five subspecies or
varieties being recognized depending on taxonomic reference (Munz, 1968; Hickman,
1993). Two of the subspecies are truly monocarpic (semelparous), whereas three are
polycarpic (Haines, 1941; Wimber, 1958). Within the San Bernardino basin, two
varieties, Yucca whipplei var. whipplei (a semelparous variety) and Yucca whipplei var.
caesitosa (an iteroparous variety), overlap in distribution (Haines, 1941). The taxonomic
relationship between these varieties allows us to determine how significantly different life
history strategies affect fecundity.

Yucca whipplei produces a large floral display following several years of
vegetative growth, with the inflorescence ranging in size from 2 to 4 m tall depending on
the variety (Haines, 1941). The single panicle contains between one hundred and several
thousand hermaphroditic flowers, which progressively open from the bottom to the top of
the inflorescence (Aker, 1982a). The flowers are pollinated primarily by the moth
Tegeticula maculata (Lepidoptera: Prodoxidae; Wilder, 1964; Udovic, 1981). A
significant difference exists between the number of flowers that are pollinated and the
number of fruit that develop and are maintained by the inflorescence; variation in the ratio
of mature fruit to the number of pollinated flowers appears to be correlated with inflorescence size (Udovic, 1981). Specific germination requirements for seeds and the conditions for seedling establishment appear to differ among the varieties.

In this study, the iteroparous Yucca whipplei var. caespitosa was compared to the monocarpic (semelparous) Yucca whipplei var. whipplei to test the hypothesis that there are differences in seed production and viability for closely related plants with iteroparous or semelparous life history strategies. The hypothesis predicts that there are trade-offs between seed production (the number of seeds and seed viability) and the production of accessory reproductive structures (inflorescence, flowers, etc.). In addition, the hypothesis predicts that there will be a trade-off between seed production and future adult survival for the iteroparous variety as compared to the semelparous variety.

Materials and Methods

Four populations of Yucca whipplei (Liliaceae, Torrey) were sampled within the southwestern section of San Bernardino County, CA. The semelparous, monocarpic Yucca whipplei var. whipplei was sampled on plots in Day Canyon (34° 10’ N, 117° 32’ W, 893 m), north of the city of Etiwanda, and in Lytle Creek (34° 10’ N, 117° 26’ W, 850 m), north of the city of Fontana. Yucca whipplei var. caespitosa, the iteroparous, polycarpic yucca, was sampled on plots in Cajon Wash (34° 11’ N, 117° 24’ W, 855 m), on private land adjacent to the Regional Campground at Glen Helen, and at Silverwood Lake State Recreation Area (34° 17’ N, 117° 19’ W, 1126 m). Plots were dominated by
Adenostoma fasciculatum, Salvia melifera, Eriogonum fasciculatum, Marrubium vulgare and Quercus sp.

Yucca rosettes within each population were chosen by randomly selecting numbered individuals from previously marked inflorescences in each experimental plot. Leaf surface area was determined by sampling random individuals from all four populations, and measuring leaf geometry. The leaves form a rectangle for over 2/3 of the length of the blade, and the remaining 1/3 is an equilateral triangle. Fifty leaves were sampled and length, width and surface area were measured for each variety. Individual rosettes sampled for the remainder of the study had leaf surface area determined by measuring the length of twenty blades within the rosette, counting the total number of blades present within the rosette, and extrapolating leaf surface area from the mean blade length (and subsequent regressions for surface area) to the whole rosette.

Leaf area index (LAI) was measured as the leaf surface area over the projected area of the rosette (Nobel, 1991). Shaded ground area was determined for each individual by measuring the diameter of the circular rosette and calculating the ground area covered. For the iteroparous variety, shaded ground area was determined for each attached rosette, and summed to determine total shaded ground area for the individual. Leaf area index was determined for both the single flowering rosette and all connected rosettes for Yucca whipplei var. caespitosa.

Inflorescence characteristics were measured for twenty five flowering rosettes for each variety. The diameter at the base of the inflorescence and the height of the inflorescence was measured to produce a regression of base diameter to inflorescence
height in order to rapidly and non-destructively measure inflorescence height. The total number of bracts on the inflorescence, the number of flowers, the number of matured fruit, and the number of seeds of each individual were counted for both varieties to assess differences in reproductive expenditure. The total number of flower scars were counted both for each individual bract, and for the inflorescence as a whole, as the flowers reaching anthesis leave a distinctive scar on the inflorescence. The number of mature fruit was determined by counting the number of fruit capsules on the inflorescence.

A total of 10 fruit capsules were sampled to measure the mean number of seeds per capsule for each inflorescence. The number of seeds produced by a particular fruit can be determined by counting the number of placental scars left on the false septum of the locule after seed removal (Aker, 1982b). During the 1994 flowering period, regressions of the number of seeds present and the length of the locule were generated, by measuring the length and number of seeds for 30 fruit of each variety to be used in this study as a non-destructive measure of the number of seeds per locule. A total of 100 seeds were removed from the fruit capsules of each sampled inflorescence to determine the dry mass of seeds for individual rosettes.

An additional 100 seeds from each inflorescence were collected to determine seed viability. A sample from each individual plant was subjected to staining with 2,3,5 - triphenyl 2H-tetrazolium chloride (TTC) which turns red in the presence of NADH dehydrogenase activity (Kearns and Inouye, 1993). In addition, twenty seeds from each individual were germinated on wet filter paper in sealed Petri dishes exposed to a 16 hour day at 22° C. The number of seeds germinated for each variety was counted daily.
Total seed production was determined for each individual of both varieties from initial measurements of the number of flowers produced, the number of fruit produced, the total number of seeds per fruit, and seed viability. In addition, estimates of seed production per unit leaf surface area were determined; for the polycarpic Y. w. var. caespitosa all attached rosettes were included in measurements of leaf surface area.

All values of leaf surface area, leaf area index, seeds per fruit, flowers per inflorescence, total viable seeds, inflorescence height, and seed viability were compared between populations and varieties of yucca through the nonparametric Kruskall-Wallis Rank Sum test. Also, combined values for the populations of each variety were compared by student’s t-test and Mann-Whitney Rank Sum tests. Statistics were performed with SigmaStat software (Jandel Scientific Corp). Data are expressed throughout the results as mean ± 1 SE.

Results

Leaf surface area increased significantly as a function of increasing leaf length for both Y. w. var. whipplei and Y. w. var. caespitosa (Table 2.1). There were no significant differences between this technique and tracing the surface area of the leaves on paper along with recording the thickness of individual leaves (paired t-test, \( N = 20, P < 0.05 \)). Inflorescence height increased as a function of the size of the diameter of the inflorescence at its base and the number of seeds per fruit capsule was correlated to the length of the fruit capsule. These regressions (Table 2.1) provided a quick and simple means of
measuring inflorescence height, leaf surface area and seeds per fruit in the field without destructive harvesting.

For flowering rosettes of the two varieties, mean leaf surface area was $11 \pm 0.7 \, \text{m}^2$ for \textit{Y. w. var. whipplei} and $3.59 \pm 0.12 \, \text{m}^2$ for individual rosettes of \textit{Y. w. var. caespitosa}. However, when the surface area of the attached rosettes was included, the mean leaf surface area for the iteroparous variety was not significantly different compared to that for the semelparous variety (Table 2.2). Flowering individuals of the iteroparous \textit{Y. w. var. caespitosa} had a mean of $2.65 \pm 0.15$ attached rosettes per plant. Leaf area index (leaf surface area / shaded ground area) significantly differed between varieties (Mann-Whitney Rank Sum test, $N = 80$, $P < 0.01$, Table 2.2). The mean value for leaf area index for individuals of \textit{Y. w. var. whipplei} was $8.0 \pm 0.44$ while the value was $1.58 \pm 0.11$ for \textit{Y. w. var. caespitosa}, however, the total leaf area index of all attached rosettes was $2.65 \pm 0.22$. The majority of this difference was due to the greater leaf surface area of the semelparous plant compared to the iteroparous rosette, and not due to the amount of ground that was shaded for each variety. Nearly twice the number of leaves were present on the flowering rosettes of \textit{Y. w. var. whipplei} than on \textit{Y. w. var. caespitosa} ($464 \pm 12.5$ and $288 \pm 9.5$ leaves, respectively; Mann-Whitney Rank Sum test, $N = 80$, $P < 0.001$). However, when the adjacent rosettes were included, \textit{Y. w. var. caespitosa} had significantly more leaves per individual than \textit{Y. w. var. whipplei} ($781 \pm 58$ per individual; student’s t-test, $df = 78$, $P > 0.001$).

For the different populations of \textit{Yucca whipplei} there were no significant differences in mean inflorescence height (Mann-Whitney Rank Sum test, $N = 40$, $P >$.
0.05). However, significant differences in inflorescence height were found between the two varieties of *Yucca whipplei* (Table 2.2). The iteroparous *Y. w*. var. *caespitosa* produced a 20% smaller reproductive stalk than the semelparous *Y. w*. var. *whipplei*, with a mean length of 3.70 ± 0.03 m for *Y. w*. var. *whipplei* (Day Canyon and Lytle Creek), compared to 3.05 ± 0.06 m for both populations of *Y. w*. var. *caespitosa* (Mann-Whitney Rank Sum test, *N* = 80, *P* < 0.0001, Table 2.2).

*Yucca whipplei* var. *whipplei* produced nearly twice the number of flowers per inflorescence compared to *Y. w*. var. *caespitosa* (1600 ± 69 and 981 ± 82, respectively, Mann-Whitney Rank Sum test, *N* = 80, *P* < 0.0001, Table 2.2). This increase in total flowers per stalk was partially a function of an increase in the mean number of flowers per bract for *Y. w*. var. *whipplei* compared to *Y. w*. var. *caespitosa* (9.4 ± 0.12 and 8.58 ± 0.1, respectively). There was a significant difference in the number of seed-bearing fruit produced by the two varieties. *Yucca whipplei* var. *whipplei* produced over three times the number of fruit per inflorescence than *Y. w*. var. *caespitosa* (Table 2.2). The fruit to flower ratio was 0.094 ± 0.001 for *Y. w*. var. *whipplei* as compared to 0.050 ± 0.001 for *Y. w*. var. *caespitosa*.

There was a significant difference in the number of seeds that germinated for the two varieties of *Yucca whipplei* (*N* = 80, *P* < 0.01, Table 2.2). *Yucca whipplei* var. *whipplei* produced seeds which germinated at a rate of 5% d⁻¹ compared to 3.12% d⁻¹ for *Y. w*. var. *caespitosa* (Fig. 2.1). Seeds of *Y. w*. var. *whipplei* began to germinate after 5 d whereas germination for seeds of *Y. w*. var. *caespitosa* began germinating after 8 d. Furthermore, a greater number of *Y. w*. var. *whipplei* seeds stained in the presence of
TTC than for *Y. w. var. caespitosa* (Mann-Whitney Rank Sum test, \(N = 80, P < 0.01\); Table 2.2).

For *Y. w. var. whipplei*, there was a decrease in the percentage of viable seeds as inflorescence size increased (Fig. 2.2). Smaller inflorescences (less than 3.6 m in height) exhibited seed viability of \(92 \pm 0.3\) % viable seeds, whereas large inflorescences (greater than 3.6 m in length) produced seeds which were \(82 \pm 0.25\) % viable. A similar relationship was not exhibited by *Y. w. var. caespitosa*. The total number of viable seeds produced by an individual of *Y. w. var. whipplei* logarithmically increased as leaf surface area increased (Fig. 2.3). Initially, small increases in leaf surface area of the flowering rosette resulted in large increases in the production of viable seeds per individual according to the equation of the regression line (the total number of viable seeds = \(-23 (\text{leaf surface area})^2 + 160 (\text{leaf surface area}) - 1264\), \(N = 40, r^2 = 0.51, P < 0.05\)).

Increases in the number of viable seeds produced by the iteroparous variety occurred with increases in the leaf surface area of the individual. Specifically, as *Y. w. var. caespitosa* increased the number of attached rosettes, the mean number of viable seeds produced per inflorescence increased (Fig. 2.4). The number of viable seeds per inflorescence increased from 1750 ± 260 to 4270 ± 130 viable seeds per individual as the total number of rosettes per individual increased from one to four.

There were significant differences in the total number of viable seeds on a leaf area basis produced by the two varieties in a single reproductive event (Table 2.3). *Yucca whipplei* var. *whipplei* produced a mean of \(14.9 \pm 0.77\) fruit per m\(^2\) whereas *Y. w. var. caespitosa* produced a mean of \(6.7 \pm 0.94\) fruit per m\(^2\) for all attached rosettes (Table 2.3).
Yucca whipplei var. whipplei produced a mean of $123 \pm 1.92$ seeds per fruit with a mean viability of $82.5 \pm 4.1\%$, which equates to $15000 \pm 1001$ viable seeds per plant. For a mean of $128 \pm 4$ seeds per fruit and a mean of $62.7 \pm 2.9\%$ viable seeds, Y. w. var. caespitosa produced $2900 \pm 184$ viable seeds per reproductive event. There were also differences in the number of seeds produced per leaf surface area of the plant (Table 2.3). Yucca whipplei var. whipplei produced $1452 \pm 119$ seeds per m$^2$ of leaf surface area, whereas Y. w. var. caespitosa produced $322 \pm 75$ seeds per m$^2$.

Discussion

Individuals of Y. w. var. whipplei produced larger inflorescences, with more flowers and more seed-bearing fruit than did individuals of Y. w. var. caespitosa. The number of flowers on an inflorescence is highly correlated with the basal area of the rosette for Yucca whipplei (Aker, 1982b). In the present study, a relationship was also found between the number of viable seeds and leaf surface area for Y. w. var. whipplei as well as viable seed number and the number of rosettes for Y. w. var. caespitosa. For both varieties, plants with a greater resource base (leaf surface area or the number of attached rosettes) had greater production of viable seeds. For Lobelia keniensis, individuals with several attached rosettes are more likely to flower with greater frequency than plants with fewer rosettes (Young, 1984). In contrast, individuals of Asclopia syriaca are capable of producing several inflorescences, with fewer fruit produced as inflorescence number increases (Willson and Rathcke, 1974). Yucca whipplei var. caespitosa appears to
allocate energy from current reproduction to future adult survival and to the production of adjacent rosettes; eventually the additional leaf surface area contributes to greater fecundity per reproductive event. On the other hand, the iteroparous variety may be spreading reproduction over time to lessen the effects of unfavorable conditions for pollinator activity, seed germination and seedling establishment (Willson and Rathcke, 1974). The trade-off in seed production for these two varieties of *Yucca whipplei* is similar to the trade-offs observed for *Lobelia telekii* (a semelparous species) and *Lobelia keniensis* (an iteroparous species) with respect to resource base, the production of seeds and adult mortality (Young, 1984). In the present study, the semelparous variety maximizes seed production with increases in resource base whereas the iteroparous variety does so at a lesser rate. This is consistent with the prediction of the hypothesis that there would be a trade-off between current seed production and future survival for the iteroparous variety.

Because reproduction requires the majority of translocatable resources in *Yucca whipplei* (Webber, 1965; Udovic and Aker, 1981), the amount of such resources can be used to determine the total cost of flowering and should be related to reproductive expenditure (Udovic and Aker, 1981; Aker, 1982b). Leaf surface area is often representative of the amount of photosynthate a plant is able to produce, as it indicates light interception and CO₂ uptake ability (Noble, 1991). While there was no significant difference in the resource base (leaf surface area) for the two varieties, there was a significant difference in the overall morphology (based on leaf area index), with *Y. w. var. whipplei* having nearly double the surface area for light interception and CO₂ uptake per
unit ground area as *Y. w. var. caespitosa*. This difference in the ability to intercept light and take up CO₂ may help in the production of more photosynthate (Larcher, 1995), and thus produce greater numbers of viable seeds for the semelparous variety compared to the iteroparous variety. On the other hand, carbon limitations may not be as critical as nitrogen use efficiency in the production of viable seeds in *Yucca whipplei* (Larcher, 1995), as nitrogen is often a limiting factor in seed production (Tilman, 1988).

Based on the size of the inflorescence, the number of flowers, or the number of fruit produced by the individual, an estimate of reproductive expenditure can be made (Udovic, 1981). The expenditure that the iteroparous variety places into a particular reproductive event is considerably less than for the semelparous variety. Indeed, semelparous individuals should maximize current fecundity while iteroparous individuals conserve resources for future reproductive episodes (Lloyd, 1980). Our findings are consistent with the hypothesis that the reproductive event would be allocated less resources in the iteroparous compared to the semelparous species.

The number of seeds produced per unit leaf surface area differed for the two varieties. The semelparous variety produced significantly more seeds per unit leaf surface area than the iteroparous variety. This trade-off between the varieties (and life history strategies) in the production of viable seeds may represent a difference in the way that resources are allocated to reproduction. Two closely related *Lobelia* species exhibit a similar relationship with the iteroparous species exhibiting a trade-off between making seeds and future survival (Young, 1984 and 1990). *Lobelia keniensis* (an iteroparous species) produces fewer seeds than *Lobelia telekii* (a semelparous species) but reproduces
over multiple years and has a longer lifespan (Young, 1990). Even when a single rosette of \textit{Y. w.} var. \textit{caespitosa} flowers, it does not produce as many seeds per leaf surface area as \textit{Y. w.} var. \textit{whipplei} and apparently withholds resources for the production of additional stems for future survival. There appears to be a trade-off between inflorescence size and the percentage of total viable seeds produced for \textit{Y. w.} var. \textit{whipplei}. According to the principle of allocation, resources placed into the production of accessory reproductive structures (such as an inflorescence) are at the cost of another structure. Young (1984) found a close link between inflorescence height and resource limitations in \textit{Lobelia telekii}. Similar trade-offs have been reported for members of the genus \textit{Plantago}, which exhibit negative correlations between the size of fruit and the mean seed mass within the fruit (Primack, 1978). In the case of \textit{Y. w.} var. \textit{whipplei}, inflorescence size was negatively correlated with seed viability (percentage of viable seeds). However, the total number of viable seeds still increased with increasing inflorescence height. The iteroparous variety \textit{Y. w.} var. \textit{caespitosa} does not appear to have a similar trade-off, possibly due to the ability to shunt resources between adjacent rosettes. The storage of sufficient water is the major limiting factor for flowering of desert succulents (Nobel, 1977). Adjacent connected stems undergo water stress when the central rosette flowers, and shunting of water and carbon between individuals of \textit{Agave deserti} is common (Nobel, 1977; Tissue and Nobel, 1990a and 1990b). Resource translocation between rosettes may allow \textit{Y. whipplei} var. \textit{caespitosa} to evade such limitation (or at least significantly reduce such limitation) and may allow for the increase in the number of viable seeds.
Yucca whipplei var. whipplei appears to regulate its reproductive expenditure via the number of viable seeds per fruit. Aker (1982b) suggested that the determination of maternal expenditure in Yucca whipplei was at the fruiting stage of reproduction. Lloyd (1980) considered fruit determination as the last possible stage for regulation, but Aker (1982b) suggests that regulation of the number of seeds is an additional step. Aker (1982b) did not find variation in seed weight with increases in the number of matured fruit, however in the present study, viability decreases with inflorescence size and the number of fruit. The plant regulates its maternal expenditure at the last possible stage because resources are unpredictable and the plant invests all its resources on producing as many seeds as possible. When resources for reproduction are unpredictable at early stages of reproduction, plants should determine maternal investment at the latest stage possible (Lloyd, 1980). For Y. whipplei, the number of seeds and seed viability are balanced with the production of an inflorescence and the number of fruit maintained. This also suggests that there is the potential for resources received before the final development of seeds to impact viability.

In summary, there is a trade-off between future survival and seed production for the closely related varieties of Yucca whipplei. Also there is a trade-off within an individual between the energy placed into producing viable seeds and accessory reproductive structures (inflorescence height, number of flowers, and number of bracts). Yucca whipplei has been used as an example of the reproductive effort model explaining the evolution of semelparity (Young, 1990; Schaffer and Gadgil, 1975). Here we have
shown that fecundity for both varieties of *Yucca whipplei* is linked to leaf surface area and rosette number, contrary to the models that relate semelparity to plant age (Takata, 1995). Differences in reproductive strategies may impact the population dynamics of *Yucca whipplei* under a warmer and drier climate; distributions of the two varieties may change significantly, with the caespitoid variety potentially invading areas now dominated by the semelparous variety. The semelparous variety is abundant on the wetter southern facing mountain faces as compared to the northern rain shadow areas which are dominated by the iteroparous variety. Demographic models which attempt to explain the evolution and distribution of semelparity are based on disturbance rates and ultimate fecundity (based on establishment; Young and Augspurger, 1991). Because *Yucca whipplei* has been shown to be significantly affected by fire (Huxman and Loik, 1996b) and establishment may be linked to major rainfall event such as El Niño (Huxman and Loik, 1996a), altered climate has the potential to influence distribution.
CHAPTER THREE

THE REPRODUCTIVE EFFORT MODEL AND EVOLUTION OF SEMELPARIETY IN YUCCA WHIPPLEI

There are several models used to describe the evolution of semelparous and iteroparous reproduction in terrestrial plants, including a bet-hedging, a demographic, and a reproductive effort model (Schaffer and Schaffer, 1977; Young, 1990; Young and Augspurger, 1991). Semelparity is the life history phenomenon in which a single episode of reproduction is followed by rapid degeneration and death of the individual (Schaffer and Schaffer, 1977), whereas iteroparous individuals produce offspring over several reproductive events and allocate resources to ensure post-flowering survival (Schaffer, 1974). None of the models appear to be mutually exclusive, but the selective pressures described in each are extremely different (Young and Augspurger, 1991). Several organisms have been used as examples of each of the reproductive models (Schaffer and Schaffer, 1977 and 1979; Aker, 1982b; Young, 1990; Young and Augspurger, 1991). The reproductive effort model, like most theoretical population models addressing life history strategies, has been applied to closely related species within a genus (Young, 1990; Young and Augspurger, 1991). *Yucca*, *Lobelia*, and *Agave* spp. have had models applied to flower, fruit and seed production data at the species level, but there is still a need to understand the population ecology of more closely related semelparous and iteroparous
plants (Young and Augspurger, 1991). Species that differ among varieties (with respect to reproductive strategies) could provide a system upon which theoretical models could be based.

Selection for increased reproductive effort can lead to the evolution of semelparity (Schaffer and Schaffer, 1979). The reproductive effort model predicts that when there is a positive correlation between reproductive effort and reproductive success per unit reproductive effort, semelparity will be favored (Schaffer and Schaffer, 1979; Young and Augspurger, 1991). If this relationship is absent or negative, iteroparity will be favored (Schaffer and Rosenzweig, 1977; Young and Augspurger, 1991). While a correlation between theoretical predictions and empirical data has been found (Young and Augspurger, 1991), the conditions that select for increased reproductive effort have only been speculated upon in some *Agave* sp. and *Yucca* sp. (Schaffer and Schaffer 1979). The reproductive effort model (theory of optimal reproductive strategies) predicts three situations in which selection for a larger seed crop in a single reproductive event (semelparity) is favored (Schaffer and Schaffer, 1977 and 1979; Rathcke and Lacey, 1985). First, small inflorescences with small seed crops are heavily preyed upon while larger inflorescences produce sufficient numbers of seeds to overwhelm seed predators (Rathcke and Lacey, 1985). Second, pollinators forage primarily on the largest inflorescences because larger inflorescences would have a large number of flowers, and therefore, greater rewards than small inflorescences (Schaffer and Schaffer, 1977; Udovic, 1981). Third, under resource-limited conditions there is a positive correlation between reproductive effort and reproductive success per unit reproductive effort, due to the
potentially severe consequences of flowering and semelparity will be favored (Schaffer and Gadgil, 1975; Young and Augspurger, 1991).

Yucca whipplei has been described as the prime example of evolution of semelparity as described by the reproductive effort model of life history, even though a causal mechanism has not been clearly identified (Schaffer and Schaffer, 1977 and 1979; Aker, 1982b; Young, 1990; Young and Augspurger, 1991). Investigations within this species using comparisons of flower, fruit and seed production between varieties of Yucca whipplei may provide insight into the reproductive effort model. Within the species, there are several varieties which exhibit different reproductive strategies, Yucca whipplei var. whipplei is semelparous, whereas Yucca whipplei var. caespitosa is iteroparous (Haines, 1941; Wester, 1961). In this paper flower, fruit and seed production from both varieties tests the ability of the reproductive effort model to describe the flowering pattern of Yucca whipplei. The hypothesis that the semelparous variety will display a positive correlation between fecundity per unit reproductive effort and reproductive effort, whereas the iteroparous variety will show either no relationship or a negative correlation was tested to assess the ability of the reproductive effort model to describe the evolution of semelparity.
Materials and Methods

Four populations of *Yucca whipplei* (Liliaceae, Torrey) were sampled within southwestern San Bernardino County, CA. The semelparous variety *Yucca whipplei* var. *whipplei* was sampled on plots in Day Canyon (34° 10’ N, 117° 32’ W, 890 m), and in Lytle Creek (34° 10’ N, 117° 26’ W, 850 m). *Yucca whipplei* var. *caespitosa*, the iteroparous yucca, was sampled on plots in Cajon Wash (34° 11’ N, 117° 24’ W, 855 m), on private land adjacent to the Regional Campground at Glen Helen Regional Park, and at Silverwood Lake State Recreation Area (34° 17’ N, 117° 19’ W, 1126 m). The Lytle Creek and Cajon Wash plots are within 2 km of each other. Plots were dominated by *Adenostoma fasciculatum, Salvia melifera, Eriogonum fasciculatum, Marrubium vulgare, Quercus dumosa* and *Q. chrysolepis*.

Flower, fruit and seed production data for each variety was measured by sampling flowering rosettes that were randomly chosen by selecting numbered individuals from previously marked inflorescences in each experimental plot. Leaf surface area was determined for each plant by measuring leaf geometry, counting the total number of blades present within the rosette, and extrapolating leaf surface area from the mean blade length to the whole rosette. Shaded ground area was determined for each individual by measuring the diameter of the circular rosette and calculating the ground area covered by each rosette. For the iteroparous variety, shaded ground area was determined for each attached rosette, and summed for all rosettes to determine total shaded ground area for...
the individual. This allowed leaf area index to be calculated as the leaf surface area over
the projected area of the rosette (Nobel, 1991).

The height of the inflorescence of each flowering individual (twenty from each of
four plots) was determined along with the total number of bracts on the inflorescence, the
number of flowers, the number of matured fruit, and the number of seeds. A total of 10
fruit capsules were sampled to measure the mean number of seeds per capsule for each
inflorescence. A total of 100 seeds from each inflorescence were collected to determine
seed viability by staining with 2,3,5-triphenyl 2H-tetrazolium chloride, which turns red in
the presence of NADH-dehydrogenase activity (Kearns and Inouye, 1993), and by
germinating 20 seeds from each plant on wet filter paper in sealed Petri dishes exposed to
a 16 hour day at 22°C. The number of seeds germinated for each variety was counted
daily. This double method of determining seed viability assures valid estimates for
determining the total number of viable seeds each plant produced. Total seed production
was determined for each individual of both varieties from initial measurements of the
number of fruit produced, the total number of seeds per fruit and seed viability. In
addition, seed production per unit leaf surface area and leaf area index were determined;
for the iteroparous Y. w. var. caespitosa all attached rosettes were included in these
measurements.

All values of leaf surface area, leaf area index, seeds per fruit, flowers per
inflorescence, total viable seeds, inflorescence height, and seed viability were compared
between populations and varieties of yucca through nonparametric Kruskall-Wallis Rank
Sum test. Also, combined values for the populations of each variety were compared by
student's t-test and Mann-Whitney Rank Sum tests. Data are expressed throughout the results as mean $\pm 1$ SE.

Flower, fruit and seed production data were tested against the predictions of the reproductive effort model by comparing several different parameters. Measurements of fecundity per unit reproductive effort were used to plot against measurements of reproductive effort for both varieties. The statistical relationships exhibited were compared against the predictions that semelparity will produce a positive correlation and an iteroparous individual will produce either no correlation or a negative one. Schaffer and Schaffer (1977) originally plotted the fruit to flower ratio against inflorescence height to test the assumptions of the reproductive effort model. The number of fruit produced was an estimate of fecundity, whereas the number of flowers and inflorescence height were considered to be correlated with reproductive effort (Schaffer and Schaffer, 1977 and 1979). We used these three parameters, and several additional measurements to assess fecundity and reproductive effort. In addition to fruit production, the total number of viable seeds was used as a measure of fecundity. In addition to the number of flowers and inflorescence height, leaf surface area and leaf area index were used as measures of reproductive effort.

Results

Individuals of *Y. w.* var. *whipplei* produced larger inflorescences ($3.70 \pm 0.03$ m), with more flowers ($1600 \pm 69$) and more seed-bearing fruit ($150 \pm 6.8$) than did
individuals of *Y. w.* var. *caespitosa* (3.05 ± 0.06, 981 ± 82, 55 ± 6.14, respectively; table 2.2). In addition, *Y. w.* var. *whipplei* produced nearly three times the number of viable seeds as compared to *Y. w.* var. *caespitosa*. A relationship was found between the number of viable seeds and leaf surface area for *Y. w.* var. *whipplei* as well as viable seed number and the number of rosettes for *Y. w.* var. *caespitosa*. For both varieties, plants with a greater relative resource base (leaf surface area or the number of attached rosettes) had greater production of viable seeds than plants with relatively smaller resource bases (See Table 2.2, Fig 2.3 and 2.4).

Individually, *Y. w.* var. *whipplei* produced twice as many fruit per flower (on each inflorescence) than *Y. w.* var. *caespitosa* (Table 3.1). The ratio of fruit matured over the number of flowers produced for each plant plotted against the inflorescence height were not correlated for either *Y. w.* var. *whipplei* or *Y. w.* var. *caespitosa* (Fig. 3.1). Only 9% of the variation in fruit to flower ratio was accounted for by variation in inflorescence height for *Y. w.* var. *whipplei* and only 3% for *Y. w.* var. *caespitosa*. *Yucca whipplei* var. *whipplei* produced over three times the number of viable seeds per flower as compared to *Y. w.* var. *caespitosa* (Table 3.1). The total number of viable seeds divided by the number of flowers plotted against inflorescence height did not produce a significant relationship for either variety (Fig. 3.2). *Yucca whipplei* var. *whipplei* produced about five times the number of viable seeds per leaf surface area as compared to *Y. w.* var. *caespitosa* (Table 3.1). The number of seeds per leaf surface area was negatively correlated with inflorescence height for *Y. w.* var. *whipplei*, whereas for *Y. w.* var. *caespitosa*, the number of viable seeds per leaf surface area was not a function of inflorescence height (Fig. 3.3).
For *Y. w.* var. *whipplei*, the number of fruit per leaf surface area was negatively correlated to leaf surface area, while for *Y. w.* var. *caespitosa*, the number of fruit per m² was not correlated to leaf surface area (Fig. 3.4). The number of viable seeds produced per leaf surface area for *Y. w.* var. *whipplei* was negatively correlated with leaf surface area, while for *Y. w.* var. *caespitosa*, there was not a significant relationship (Fig. 3.5). The number of viable seeds per leaf surface area also was negatively correlated to the leaf area index of the plant for *Y. w.* var. *whipplei* (Fig. 3.6). For *Y. w.* var. *caespitosa*, the number of viable seeds per m² did not change as a function of the leaf area index of the plant (Fig. 3.6).

**Discussion**

By all measurements of fecundity per unit effort plotted against reproductive effort, the flower, fruit and seed production data for *Y. w.* var. *whipplei* produced either a negative correlation or no significant relationship, as compared to *Y. w.* var. *caespitosa* which consistently produced no correlation. The observed pattern is opposite to the pattern of resource use predicted for a semelparous plant by the reproductive effort model. These results suggest that the model does not describe the evolution of semelparity in these varieties or populations of *Yucca whipplei*. According to the predictions of the model, the pattern of resource use during flowering for the semelparous variety suggests that it should be exhibiting several reproductive events over it’s lifetime. The iteroparous variety appears to be consistent with the predictions of the model.
Schaffer and Schaffer (1977 and 1979) found that the fraction of flowers that develop into fruit is a positive function of inflorescence size in the semelparous variety of *Yucca whipplei*. In addition, they found this relationship for a number of semelparous species of *Agave*. They developed a relative stalk height to make comparisons across species and genera (not needed here because of the intraspecific comparisons made) and only included 5 size classes for which mean fruit and flower production were compared. In addition, their measurement of fecundity (fruit number) with the number of viable seeds produced per fruit was found to vary significantly from individual to individual.

Because the reproductive effort model does not accurately describe the relationship between fecundity and reproductive effort, (at least for *Y. w. var. whipplei*) the conditions which give rise to semelparity are unclear for *Y. w. var. whipplei*. The three situations which are thought to select for increased reproductive effort with increasing reproductive success per unit reproductive effort (pollinator foraging behavior, seed predator satiation, and resource limitation) do not appear to explain the evolution of semelparity in *Y. w. var. whipplei*. Aker (1982b) suggested that pollinators were optimally foraging, but did not show that access to pollinators was limiting for any plants in a flowering population. Both Aker (1982b) and Schaffer and Schaffer (1977 and 1979) rejected the role of seed predators based on extensive field observations, and suggested that limitations in available resources was a driving force for the evolution of semelparity. The present data suggests that resource-based pressures are not the most important factor for the evolution of semelparity.
There is the possibility that the measurements of reproductive effort and fecundity are not appropriate. Resource allocation to reproduction has been measured in various ways, from physiological data relating respiration and photosynthesis to reproductive biomass (Doust, 1989) to correlates of these processes such as the basal area of the plant or inflorescence size (Schaffer and Schaffer, 1977; Aker, 1982b). If the measurements made here are inaccurate, appropriate physiological data are required to provide a better foundation of empirical data. For the estimates of reproductive effort used here, leaf surface area is often representative of the amount of photosynthate a plant is able to produce, as it reflects the amount of light interception and CO₂ uptake (Noble, 1991). Since flowering in Yucca sp. and Agave sp. requires the majority of available resources in the plant, this should be a good estimate of reproductive effort (Udovic and Aker, 1981).

There are several other models that attempt to describe the evolution of semelparity in Yucca whipplei: the bet-hedging model and the demographic model. The bet-hedging model describes situations in which increasing environmental variability and unpredictability favor iteroparity over semelparity (Schaffer and Rosenzweig, 1977; Orzack and Tuljapurker, 1989; Young and Augspurger, 1991). This is based on the idea that limiting reproduction to a single episode of reproduction is risky (in terms of successful establishment) in an unpredictable environment. This model applies well for annual grasses that utilize a yearly pattern of rainfall. As for it’s application for long-lived perennial plants, it is uncertain whether the assumptions of the model will match empirical data. The biogeography of Yucca whipplei suggests that this model could potentially explain the plant’s reproductive strategy. The semelparous variety is distributed on the
foothills and slopes of the south-facing ranges in southern California that receive considerably more rainfall than the areas in which the iteroparous variety is distributed (Haines, 1941). However, a coastal iteroparous variety exists and may have access to more resources. While our estimates were made in areas of sympatry, the reproductive strategy of the iteroparous variety in the outlying areas of the Mojave Desert may be advantageous as compared to the semelparous variety.

The demographic model describes the relationship between the initial vegetative growth period of an individual, the age at reproduction, and the interval of disturbance in a population (Young, 1985). Pre-reproduction survival and post-reproduction survival are balanced against the amount of time required to gain sufficient resources for flowering (Young, 1985 and 1990). In *Yucca whipplei* a weevil that bores into the inflorescence and disturbance by fire that can eliminate individuals with small seed crops and small inflorescence heights compared to the mean values for the population (Huxman and Loik, 1996b). This is not a true seed predator interaction, but a combination of disturbance factors which affects the demography of a population.

In conclusion, the characteristics of the semelparous variety do not appear to satisfy the predictions of the reproductive effort model. This suggests that the factors which give rise to increased reproductive effort may not important for the evolution of semelparity in *Yucca whipplei*. Physiological data for flowering individuals of both varieties might provide greater insight into the reproductive strategies of these two varieties of *Yucca whipplei*. In addition, there may be other different models which may help to describe the evolution of semelparity in *Yucca whipplei*. 

35
CHAPTER FOUR

SUMMARY

In the present study several hypotheses concerning the reproductive strategy of *Yucca whipplei* were addressed. Because of differences in strategies of resources allocation between current fecundity and future survival, differences in reproductive expenditure were hypothesized to occur between the semelparous and iteroparous varieties of *Yucca whipplei*. Based on optimal reproduction strategies, the semelparous variety should have greater reproductive expenditure than the iteroparous variety because the semelparous variety does not save resources for future survival. The data collected in the present study are consistent with this in that *Y. w.* var. *whipplei* concentrates its resources on one episode of reproduction that results in greater numbers of high-quality seed as compared to *Y. w.* var. *caespitosa*. Trade-offs were predicted to occur within a plant with respect to the quantity of resources that are allocated to the production of an inflorescence, flowers, fruit, and viable seeds, as plants have to balance the production of these structures with finite amounts of resources. The data collected in the present study are consistent with this hypothesis, as increases in the size of an inflorescence was made as a sacrifice to viable seed production. Viable seed production should be maximized in both varieties regardless of life history strategy. The data was consistent with this in that increased seed production was a function of increased resource base.
The data collected in this study are consistent with current ideas surrounding plant flower, fruit and seed production with respect to reproductive strategy. The data is consistent with other studies that have shown trade-offs in current seed production for future survival in iteroparous plants as compared to the same values in closely related semelparous plants (Young, 1984). The relationships between leaf surface area (resource base) and seed production for Y. w. var. whipplei is consistent with Aker (1982b) who found that fecundity is related to plant size for Yucca whipplei. Similar relationships between the number of rosettes and seed production for Y. w. var. caespitosa have been found. Trade-offs between the production of viable seeds and structures such as inflorescences are consistent with other studies of plant allocation patterns to reproduction (Willson and Rathcke, 1974).

The hypothesis was addressed that relationships between fecundity per unit reproductive effort and reproductive effort could be predicted based on life history strategy by the reproductive effort model of semelparity (Schaffer and Schaffer, 1977; Young and Augspurger, 1991). The data collected here for Y. w. var. caespitosa was consistent with the hypothesis that there would be either a negative or no correlation between fecundity per unit reproductive effort and reproductive effort. The data is not consistent with the hypothesis that a positive correlation between those two variable exists in Y. w. var. whipplei. Therefore, the evolution of semelparity in this variety of Yucca whipplei is not well described by the reproductive effort model.

The data in the present study is inconsistent with Schaffer and Schaffer (1977 and 1979) in that the model of reproductive effort theory describes the evolution of semelparity
in *Yucca whipplei*. They suggested that there are disproportionate increases in fecundity (an increase in the fruit to flower ratio) with increases in inflorescence height. The present data found a different relationship between these two variables, consistent with either the bet-hedging or demographic models that have a greater ability to describe the evolution of semelparity in hapaxanthic plants (plants that do not have distal axillary meristems; Young, 1985 and 1990; Young and Augsurger, 1991). The pattern of flowering measured here caused the rejection of the reproductive effort model and suggests the future studies addressing different models are required.

The rejection of the reproductive effort model fits well with data collected on fire disturbance and seed crop reduction for *Yucca whipplei*. Small stalks, with heavier infestation from yucca weevils, were more likely to burn than large stalks resulting in decreased seed crops for individual plants and whole populations (Huxman and Loik, 1996b). This disproportionate survival of inflorescences (with larger numbers of seeds) could lead to the enhanced fitness of plants which utilize small versus large reproductive efforts (i.e. inflorescence size and seed numbers; Schaffer and Schaffer, 1977; Rathcke and Lacey, 1985). Disturbance and establishment characteristics are important components of bet-hedging and demographic models for the evolution of semelparity (Young, 1981, 1984, and 1990). Information that can be applied to the bet-hedging and demographic models is necessary to provide a more accurate analysis of the evolution of semelparity in *Yucca whipplei*. Several key items must be measured to provide the appropriate data, including, life table analysis, analysis of disturbances, and establishment characteristics. In addition, long-term projects that measure interannual variability in flowering, resource
abundance, and disturbance will be very important in producing a better view of the
evolution of semelparity in *Yucca whipplei*. 
Table 2.1. Relationships between leaf length and area, inflorescence height and diameter, as well as number of seeds and fruit size for both varieties of Yucca whipplei. 

* N = 50 for leaf surface area to leaf length, 
* N = 20 for inflorescence height to diameter at base, 
* N = 30 for number of seeds per fruit to length of fruit.

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>Y. w. var. whipplei (semelparous)</th>
<th>Y. w. var. caespitosa (iteroparous)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaf surface area (y)</td>
<td>( y = 6.7x - 139 \ r^2 = 0.93^{**} )</td>
<td>( y = 3.17x - 48 \ r^2 = 0.95^{**} )</td>
</tr>
<tr>
<td>to leaf length (x)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Inflorescence height (y)</td>
<td>( y = 0.15x + 2.3 \ r^2 = 0.74^{*} )</td>
<td>( y = 0.27x + 1.01 \ r^2 = 0.77^{*} )</td>
</tr>
<tr>
<td>and diameter at base (x)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number of seeds per fruit (y)</td>
<td>( y = 6.5x + 1.7 \ r^2 = 0.71^{*} )</td>
<td>( y = 11.9x - 9.6 \ r^2 = 0.74^{*} )</td>
</tr>
<tr>
<td>and length of fruit (x)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* \( P < 0.05 \)
** \( P < 0.01 \)
Table 2.2. Vegetative and floral characteristics for Yucca whipplei var. whipplei and Yucca whipplei var. caespitosa. Data are means ± 1 SE, N = 40 plants. Means for Yucca whipplei var. caespitosa are from one reproductive event and all attached rosettes.

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>Variety</th>
<th>Y. w. var. whipplei (semelparous)</th>
<th>Y. w. var. caespitosa (iteroparous)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaf surface area (m²)</td>
<td></td>
<td>11.0 ± 0.7</td>
<td>9.89 ± 0.79</td>
</tr>
<tr>
<td>Leaf area index</td>
<td></td>
<td>8.0 ± 0.44</td>
<td>2.65 ± 0.22**</td>
</tr>
<tr>
<td>Inflorescence size (m)</td>
<td></td>
<td>3.70 ± 0.03</td>
<td>3.05 ± 0.06****</td>
</tr>
<tr>
<td>Number of flowers produced</td>
<td></td>
<td>1600 ± 69</td>
<td>981 ± 82****</td>
</tr>
<tr>
<td>Number of fruit produced</td>
<td></td>
<td>150 ± 6.8</td>
<td>55 ± 6.14***</td>
</tr>
<tr>
<td>Percent seeds germinated</td>
<td></td>
<td>80 ± 4</td>
<td>56 ± 3**</td>
</tr>
<tr>
<td>Percent viable seeds</td>
<td></td>
<td>82.5 ± 4.1</td>
<td>62.7 ± 2.9**</td>
</tr>
</tbody>
</table>

* $P < 0.05$
** $P < 0.01$
*** $P < 0.001$
**** $P < 0.0001$
Table 2.3. Reproductive efficiency for the two varieties of Yucca whipplei. Data are means ± 1 SE. Means from Yucca whipplei var. caespitosa are from multiple attached rosettes. LSA is leaf surface area. N = 40.

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>Y. w. var. whipplei (semelparous)</th>
<th>Y. w. var. caespitosa (iteroparous)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fruit per LSA</td>
<td>14.9 ± 0.77</td>
<td>6.7 ± 0.94*</td>
</tr>
<tr>
<td>Total viable seeds</td>
<td>15000 ± 1001</td>
<td>290.03 ± 184**</td>
</tr>
<tr>
<td>Viable seeds per LSA</td>
<td>1452 ± 119</td>
<td>322 ± 75*</td>
</tr>
</tbody>
</table>

* P < 0.01
** P < 0.0001
Table 3.1 - Fecundity per unit reproductive effort for both varieties of *Yucca whipplei* measured in the field. Data are expressed as means ± one SE. *N* = 40.

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>Variety</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td><em>Y. w. var. whipplei</em></td>
</tr>
<tr>
<td></td>
<td></td>
<td>(semelparous)</td>
</tr>
<tr>
<td>Fruit matured per flower</td>
<td>0.09 ± 0.001</td>
<td>0.04 ± 0.002**</td>
</tr>
<tr>
<td>Viable seeds per flower</td>
<td>8.7 ± 0.6</td>
<td>2.7 ± 0.1**</td>
</tr>
<tr>
<td>Viable seeds per LSA</td>
<td>1452 ± 119</td>
<td>322 ± 75***</td>
</tr>
</tbody>
</table>

* *P* < 0.05

** **P* < 0.01

*** **P* < 0.001
Fig. 2.1. The percent of seeds that germinated for *Yucca whipplei* var. *whipplei* (●) and *Yucca whipplei* var. *caespitosa* (■). Seeds were placed on wet filter paper in Petri dishes for over twenty days. Data are means ± SE, *N* = 40 plants for each variety.
Fig. 2.2. Seed viability as a function of inflorescence size for *Yucca whipplei* var. *whipplei*. (Seed viability) = -47 (Inflorescence height) + 282, N = 40, r² = 0.52, P < 0.05.
Fig. 2.3. The number of viable seeds produced by individuals of *Yucca whipplei* var. *whipplei* as a function of leaf surface area (LSA). (Viable seeds) = $-23(LSA)^2 + 1606(LSA) - 1264$, $N = 40$, $r^2 = 0.51$, $P < 0.05$. 
Fig. 2.4. The number of viable seeds produced by individuals of *Yucca whipplei* var. *caespitosa* as a function of the total number of rosettes.
Fig. 3.1. The fruit to flower ratio (a measurement of fecundity per unit reproductive effort plotted against inflorescence height (reproductive effort) for (A) *Yucca whipplei* var. *whipplei* (●) \( r^2 = 0.09 \) and (B) *Yucca whipplei* var. *caespitosa* (■) \( r^2 = 0.03 \).
Fig. 3.2. The number of viable seeds per flower as a function of the inflorescence height of (A) Yucca whipplei var. whipplei (●) \([r^2 = 0.16]\) and (B) Yucca whipplei var. caespitosa (■). \([r^2 = 0.02]\)
Fig. 3.3. The relationship between viable seeds per leaf surface area (m2) and inflorescence height for (A) Yucca whipplei var. whipplei (●) \( r^2 = 0.33; P < 0.05 \) and (B) Yucca whipplei var. caespitosa (■). \( r^2 = 0.07 \)
Fig. 3.4. The relationship between the number of fruit per leaf surface area and leaf surface area for (A) Yucca whipplei var. whipplei (●) \[r^2 = 0.06\] and (B) Yucca whipplei var. caesitosa (■). \[r^2 = 0.26\]
The relationship between the number of viable seeds per leaf surface area and the leaf surface area of (A) *Yucca whipplei* var. *whipplei* (●) \[r^2 = 0.59; P < 0.05\] and (B) *Yucca whipplei* var. *caespitosa* (■). \[r^2 = 0.24\]
Fig. 3.6. The relationship between the number of seeds per leaf surface area and leaf area index of (A) Yucca whipplei var. whipplei (●) \( [r^2 = 0.65; P < 0.01] \) and (B) Yucca whipplei var. caespitosa (■) \( [r^2 = 0.05] \).
LITERATURE CITED


