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**Adaptation, history, and development in the evolution of a
desert annual life history**

Fox, Gordon Allen, Ph.D.

The University of Arizona, 1989

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ADAPTATION, HISTORY, AND DEVELOPMENT IN
THE EVOLUTION OF A
DESERT ANNUAL LIFE HISTORY

by

Gordon Allen Fox

A Dissertation Submitted to the Faculty of the
DEPARTMENT OF ECOLOGY AND EVOLUTIONARY BIOLOGY

In Partial Fulfillment of the Requirements

For the Degree of

DOCTOR OF PHILOSOPHY

In the Graduate College

THE UNIVERSITY OF ARIZONA

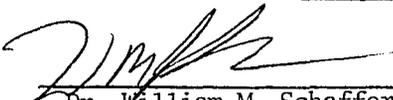
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desert annual life history

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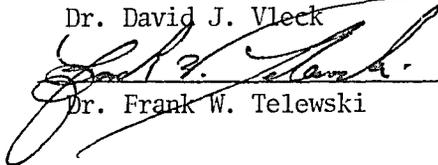
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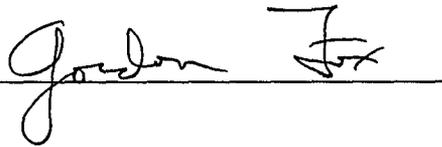
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SIGNED: _____

A handwritten signature in cursive script, appearing to read "Gordon Fox", is written over a horizontal line. The signature is written in dark ink and is positioned to the right of the word "SIGNED:".

Dedicated to C.J. Stine, D.D.S., Sc.D.,
who inspired me to become a biologist.

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ABSTRACT

Individuals of *Eriogonum abertianum* Torr. (Polygonaceae) flower in spring, or following onset of summer rains, or both. Within populations flowering time is mainly environmentally determined: there is little genetic variance for flowering time, and experimental moisture limitation significantly delays flowering.

In the field a Sonoran Desert population experienced significantly more mortality during the foresummer droughts, and had a significantly greater proportion of spring-flowering plants, than a Chihuahuan Desert population. Greenhouse experiments suggest a genetic basis for differences in size and time of flowering between these populations. Fossil and biogeographic evidence support an adaptive interpretation of earlier flowering in the Sonoran Desert.

A model of selection comparing spring-plus-summer flowering with spring-only flowering suggests that expected summer fecundity may not offset the risk of foresummer mortality in the Sonoran population. Rather than switching to a spring-only habit as predicted by the model, the species' range ends where summer rainfall declines abruptly. The invariance of the spring-plus-summer habit is not explained by the demographic, historical, or genetic data.

Plants which live for more than a year in the wild have offspring which, in the greenhouse, live longer than the offspring of the general population. This suggests a genetic basis for the occasional observed perennation. Analysis of a quantitative genetic model suggests that when adult survivorship is low, selection will generally reduce perennation. The annual habit is thus likely to persist even in the presence of genetic variation for perennation.

Optimal control models of plant carbon allocation are extended to include within-season mortality and allometric growth constraints. When parameters are varied in numerical experiments, resulting predictions for easily measurable characters (e.g., time to first flower) often vary only slightly; most differences are in fitness, suggesting that satisfactory empirical tests may be difficult to conduct. Arbitrary mortality functions can optimally lead to multiple flowering episodes, and this can depend sensitively on parameter values. Optimal trajectories with allometric constraints are divided into a period of vegetative growth and another period of mixed growth.

CHAPTER ONE

Consequences of Flowering Time Variation in a Desert Annual: Adaptation and History

Introduction

The evolution of desert annuals has usually been interpreted in purely adaptive terms, without reference to historical or phylogenetic factors (e.g., Gleason & Cronquist 1964, Schaffer & Gadgil 1975, Mulroy & Rundel 1977, Orians & Solbrig 1977a, Silvertown 1982). Annuals do compose a large fraction of the flora in hot deserts, and this fraction tends to increase with environmental variability (Gleason & Cronquist 1964, Schaffer & Gadgil 1975). The adaptive view is persuasive because the same pattern is seen among unrelated plant taxa in hot deserts around the world (Orians & Solbrig 1977b, Gutterman 1982), because the annual habit is believed to be derived in most angiosperm taxa (Stebbins 1974), and because most desert annual taxa in particular are thought to be recently derived from perennial ancestors (Johnson 1968, Axelrod 1979).

The evolution of desert annual life histories might then seem to be a case in which historical explanation can add little to the insight gained from purely adaptive considerations (see MacArthur 1972, ch. 9; Lauder 1982). Yet there are phylogenetic biases in desert plant life histories. In the Sonoran Desert, for

example, there are few or no annual Liliaceae, and no annual Agavaceae or Cactaceae; moreover, annual Cruciferae, Boraginaceae, and Hydrophyllaceae are almost entirely winter annuals, while annual Nyctaginaceae are almost entirely summer annuals.

Can we hope to understand desert annual life histories without historical or phylogenetic data? Here I consider this issue by examining life history variation among populations of the desert annual *Eriogonum abertianum* Torr. (Polygonaceae). This species has a complex phenology: individuals may flower in spring, summer, or both seasons. There is considerable mortality between spring and summer flowering episodes, because severe droughts characterize the foreshummer period. Is the risk of mortality offset by the expectation of added fecundity if an individual does survive to the summer? I present a static, purely adaptive model that predicts the circumstances under which plants with one or two flowering seasons have greater fitnesses, and then compare these predictions to field data. This purely adaptive interpretation is then compared with one based on the phylogeny and historical biogeography of this species. The demographic data are also used to consider a specific prediction about the mechanisms underlying the multiple flowering seasons.

Study species

E. abertianum germinates exclusively in response to winter rains (Christou 1974; Whitson 1975, 1976; Davidson 1977; Inouye 1980; Davidson et al. 1985). Individuals may flower in spring, summer, spring and summer, or neither season. Since surviving plants always flower in the summer, I use a simple dichotomy to categorize individuals. Plants which flower in spring are called "spring-flowerers;" surviving spring-flowerers resume flowering after onset of summer rains (i.e., survivors flower twice, non-survivors once in spring). Plants which do not flower in spring are called "non-spring-flowerers;" surviving non-spring-flowerers begin flowering after onset of summer rains (i.e., survivors flower once in summer, non-survivors do not flower).

The spring-flowering status of individuals within populations may be largely environmental in origin. Similar complex phenologies are found in virtually all annual *Eriogonum* spp. (Reveal 1969, 1978). Both spring-flowering and non-spring-flowering plants can be found in almost all *E. abertianum* populations, but these populations do not all show genetic variation for flowering time or size in the greenhouse (chapter 2). Perhaps most importantly, moisture limitation delays onset of flowering in the greenhouse (chapter 2). This indicates that spring-flowering may be partly a consequence of water status, suggesting the prediction that spring-flowerers should have greater survivorship to summer than

non-spring-flowerers. Since plant size is correlated with survivorship and with chance of flowering in spring, I compare below the survivorship of spring-flowering and non-spring-flowering individuals within size classes.

While onset of flowering of an individual may be strongly influenced by the environment, there is reason to suspect that the probability of flowering in the spring has been subject to natural selection. Since the Sonoran Desert is considerably hotter and drier than the Chihuahuan Desert, plants are less likely to survive to the summer. Sonoran Desert populations have a greater proportion of spring-flowerers than Chihuahuan Desert populations (chapter 2; table 1.1). Since differences in frequency of spring-flowering might be explained by differences in size, I compare sizes of spring-flowerers and non-spring-flowerers for the study populations. I examine the significance of variation among populations in frequency of spring-flowering with a simple model.

The Model

The model formalizes the question raised above: is the risk of mortality between seasons offset by the expected fecundity gain during the second reproductive episode? I assume that spring-flowering status of individuals is environmentally determined as suggested above, and therefore compare the

Table 1.1. Life history characteristics of two populations of *E. abertianum*.

| Variable | Organ Pipe | | Portal | |
|-------------------------------------|---|--|--|---|
| | 1985 | 1986 | 1985 | 1986 |
| Proportion | | | | |
| spring flowerers <i>N</i> = | 0.21 ^{a,b} 244 | 0.24 ^{c,b} 1380 | 0.03 ^{a,d} 510 | 0.03 ^{c,d} 1401 |
| Mean (se) height in spring | | | | |
| Spring-flowerers <i>N</i> = | 2.50 ^e (0.10) 55 | 3.10 ^f (0.03) 331 | 4.40 ^g (0.02) 69 | 4.80 ^h (0.18) 43 |
| Non-spring-flowerers <i>N</i> = | 1.50 ^e (0.04) 189 | 1.70 ^f (0.02) 1047 | 2.20 ^g (0.06) 265 | 1.70 ^h (0.02) 1358 |
| Mean (se) spring involucre | | | | |
| per spring-flowerer <i>N</i> = | 1.12 ⁱ (0.04) 102 | 2.80 ^j (0.44) 337 | 1.04 ⁱ (0.02) 74 | 1.24 ^j (0.09) 39 |
| per plant <i>N</i> = | 0.29 ^k (0.03) 390 | 0.68 ^l (0.11) 1400 | 0.04 ^k (0.01) 510 | 0.03 ^l (0.01) 1401 |
| Mean (se) summer involucre | | | | |
| per surviving plant <i>N</i> = | 7.36 ^m (1.41) 45 | 16.60 ⁿ (3.90) 42 | 107.65 ^m (11.52) 55 | 17.80 ⁿ (1.14) 327 |
| Mean (se) total involucre | | | | |
| per flowerer <i>N</i> = | --- | 4.37 ^o (0.66) 352 | --- | 17.22 ^o (1.12) 338 |
| per plant <i>N</i> = | --- | 1.10 ^p (0.17) 1400 | --- | 4.14 ^p (0.33) 1401 |
| Cumulative survivorship (se) | | | | |
| to summer <i>N</i> = | 0.01 ^{q,r} (0.003) 813 ₋ | 0.03 ^{r,s} (0.004) 1400 ₋ | 0.65 ^{q,t} (0.02) 510 ₋ | 0.26 ^{r,t} (0.01) 1401 ₋ |

- * Number of plants marked in study; for confidence limits or other statistics, harmonic mean of *N* should be used. Harmonic means are: Organ Pipe, 176.93 (1985), 131.08 (1986); Portal, 316.28 (1985), 474.36 (1986).

Statistical tests: all χ^2 df=1, df for F statistics given for each test.

a: $\chi^2=83.25$, $p<0.0001$; b: $\chi^2=1.04$, $p=0.3078$; c: $\chi^2=271.58$, $p<0.0001$; d: $\chi^2=0.023$, $p=0.8795$; e: $F=51.86$, $p<0.0001$, $df=1,242$; f: $F=560.69$, $p<0.0001$, $df=1,1377$; g: $F=145.70$, $p<0.0001$, $df=1,332$; h: $F=3037.21$, $p<0.0001$, $df=1,1401$; i: $F=1.95$, $p=0.1641$, $df=1,172$; j: $F=1.43$, $p=0.2323$, $df=1,376$; k: $F=96.38$, $p<0.0001$, $df=1,898$; l: $F=32.93$, $p<0.0001$, $df=1,2800$; m: $F=61.25$, $p<0.0001$, $df=1,98$; n: $F=0.11$, $p=0.7373$, $df=1,367$; o: $F=100.11$, $p<0.0001$, $df=1,688$; p: $F=65.87$, $p<0.0001$, $df=1,2800$; q: $\chi^2=292.1$, $p<0.0001$; r: $\chi^2=247.6$, $p<0.0001$; s: $\chi^2=1.98$, $p=0.1593$; t: $\chi^2=245.73$, $p<0.0001$;

average fitness of such spring-plus-summer plants with the fitness of hypothetical spring-only plants.

Assume that two discrete growing seasons occur in a year, and that the germination fraction is fixed. Let s_{ij} be the i th season fecundity of a plant which can live for j seasons. Assume that all spring-only plants flower in spring, but only a fraction p of spring-plus-summer plants flower in spring. Further assume that all plants survive to spring but only a fraction l of spring-plus-summer plants survive to summer. Then spring-only plants have an expectation of setting s_{11} seeds, while spring-plus-summer plants have expectations of setting ps_{12} seeds in spring and ls_{22} in summer. The mean seed set of a spring-plus-summer plant in a given year is greater than that of a spring-only plant when

$$ls_{22}g_2 + ps_{12}g_1 > s_{11}g_1, \quad (1)$$

where the g_j 's are seed survivorships from the j th season to the beginning of the next generation. Note that the limiting case of summer-only flowering occurs with $p=0$. Also note that eq. (1) could be used to compare summer-germinating plants which survive to the winter, with summer-germinating plants which flower in summer only; both syndromes occur in Sonoran Desert annuals (chapter 2).

Equation (1) depends on seed survivorship, but the tiny size of *E. abertianum* seeds (ca. 5×10^{-4} g; unpubl. data) made field measurement of seed survivorship impractical. However, seed survivorship undoubtedly declines with

the length of time seeds are on the ground. Therefore g_2 will generally be $> g_1$, although this can depend on the shapes of the two survivorship curves. In the present case, there are two specific reasons to assume $g_2 > g_1$. First, granivorous ant activity -- probably the main source of seed mortality -- peaks during the summer (Davidson 1977; pers. obs.). Second, summer seeds are deposited no more than ca. 6 wk prior to the first germination event for the next year, and some seeds often begin germinating while others are still being shed by senescent maternal plants (pers. obs.). Seeds are assumed to have equal probabilities of germinating the following winter. This may be a reasonable assumption since there is little seed dormancy in this species: more than 80% of seeds germinate in the greenhouse during their first winter (Davidson et al. 1985).

Rearranging (1) gives

$$g_2/g_1 > (s_{11} - ps_{12})/(ls_{22}) \quad (2)$$

By the assumption that $g_2 > g_1$, the left hand side of (2) is > 1 . The inequality then clearly holds regardless of the seed survivorship terms if the right hand side of (2) is < 1 . If the right hand side of (2) is ≥ 1 , we can solve for the range of values of g_2 and g_1 under which (2) would hold.

This model concerns mean seed set within a single year, but a more appropriate estimate of fitness for an annual plant is the geometric mean of

seed yield per germinating seed (Cohen 1967). This has not yet been estimated for any annual plant population. It is nevertheless possible to make some inferences with a few assumptions. I assume that spring-plus-summer plants experience greater variance in fitness among years than do spring-only plants. This is a reasonable assumption because spring-plus-summer plants must survive the foresummer drought (which varies greatly in length and severity (Bryson 1957, Sellers & Hill 1974)) before completing reproduction, while spring-only plants do not confront this risk. This is equivalent to the more formal statement that $\text{var}(s_{11})$ and $\text{var}(s_{12})$ are expected to be of the same magnitude, but variance in fitness of spring-plus-summer plants includes the additional factors $\text{var}(l)$ and $\text{var}(s_{22})$. The same conclusion can be reached by noting that since fecundity and survivorship are positively correlated with moisture availability (see below; chapter 2), s_{12} , s_{22} , and l are positively correlated with one another; if $\text{var}(s_{11})$ is again assumed to be of the same magnitude as $\text{var}(s_{12})$, spring-plus-summer plants again experience more variance in their fitness. Variance always decreases the geometric mean of a distribution. If each side of eq. (1) is approximately normally distributed (or in most cases, if each side of eq. (1) is distributed in the same family of distributions), a long-term advantage for spring-plus-summer plants requires that they have greater arithmetic mean seed set than spring-only plants.

Materials and Methods

Study sites

The Chihuahuan Desert (southeastern Arizona) study population was located at 1310 m elevation on the lower Cave Creek bajada of the Chiricahua Mts., near Portal, Arizona. The Sonoran Desert (southwestern Arizona) population was located at 835 m elevation on a rocky south-facing slope of the Ajo Mts. at Organ Pipe Cactus National Monument. These sites are hereafter referred to as Portal and Organ Pipe. The Portal site has been described by Davidson et al. (1985).

In southern Arizona there is a strong gradient from east to west of decreasing total annual rainfall, increasing variability of rainfall, later onset of summer rains, and decreasing percent of rainfall received during the summer (Bryson 1957, Sellers and Hill 1974). Since mean elevations also decrease from east to west, average temperatures increase along this gradient. The summer monsoon rains occur generally from late June or early July until September at Portal, but are largely restricted to late July and August at Organ Pipe; the total amount of summer rainfall also decreases abruptly to the west of the Ajo Mt. region of the National Monument (R.P. Neilson unpubl.; Ezcurra & Rodrigues 1986). The Portal and Organ Pipe sites thus differ in mean conditions,

seasonality, and predictability of rainfall. Climate data for the nearest U.S. Weather Service stations are given in fig. 1.1; these data exaggerate the between-site differences somewhat because the Organ Pipe weather station is at a lower elevation (511 m), and the Portal weather station at a higher elevation (1642 m), than the study sites.

Probably as a result of this climatic gradient, populations of *E. abertianum* are increasingly isolated from east to west. In southeastern Arizona, *E. abertianum* populations are generally found between and at the bases of mountain ranges. From south-central Arizona and north-central Sonora to the west, these plants are generally confined to desert mountain ranges.

The Organ Pipe site is near the western limit of the range of this species. *E. abertianum* has been reported within the National Monument only from the Ajo Mts. and from the Bates Mts. some 15 km to the northwest (Bowers 1980). No specimens from west of the Ajo Mts. are in the herbaria of the University of Arizona, Desert Botanical Garden, Rancho Santa Ana Botanical Garden, or University of California, Berkeley. The species does not occur in the Gran Desierto or Sierra Pinacate regions immediately southwest of Organ Pipe in Sonora (R.S. Felger, pers. comm.), and has not been reported at the Cabeza Prieta National Wildlife Refuge (S. Van Riper, pers. comm.) or Luke Air Force Range (unpubl. plant list) west of Organ Pipe in Arizona.

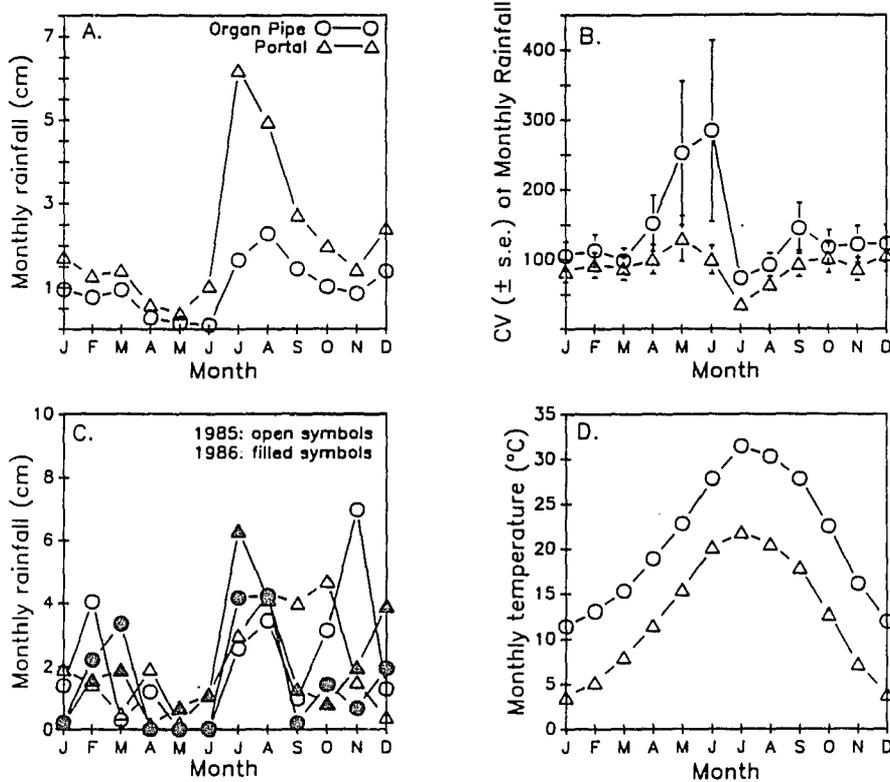


Fig.1.1. Monthly rainfall and temperature data for the Organ Pipe and Portal sites: a) Mean monthly rainfall; b) Coefficient of variation for monthly rainfall; c) Monthly rainfall during present study; d) Mean monthly temperature.

Survivorship and fecundity in the field

In 1985 and 1986, I marked plants in each population in May, after all spring flowering had begun but before drought had caused substantial mortality. At neither site in either year did I observe significant numbers of dead plants at the time of marking; dead individuals of this species usually persist in place for several months, and are readily identifiable. In both years I marked every plant on both study sites which could be individually distinguished: numbered nails were used in 1985 and numbered plastic toothpicks in 1986.

In 1986, 1400 plants were marked at each site; spring flowering status and height to highest node were recorded. At each subsequent observation (approximately monthly), survivorship, phenologic status, height, and number of involucre (flower-bearing structures) on flowering plants were recorded; observations were continued until all marked plants had died.

At Portal in 1985, 265 plants were measured at the time of marking, and an additional 245 plants were marked but not measured. Flowering status was recorded for all plants. Because frequency of spring-flowering was low, an additional 54 spring-flowerers were marked and measured; data from these plants are used below in estimates of size and fecundity of spring-flowerers, but

are excluded from estimates for the population as a whole. At Organ Pipe in 1985, plants were marked on each visit prior to the onset of summer flowering, in order to maintain a large sample. Height was measured only for the first two cohorts (150 plants on April 1, 169 plants on May 30). Because involucre are persistent, it was always possible to tell whether a plant had flowered in spring. Summer fecundity estimates for 1985 were based on counts of involucre on 55 plants at Portal in September, and 29 plants at Organ Pipe in October; at each site flower production had ceased by the time the counts occurred.

Involucre number was used for fecundity estimates because flowers are tiny (ca. 1.5 mm diameter), many per involucre, and easily abscised even before fruit maturation; the fruits are single-seeded achenes. Data from greenhouse-grown plants suggests that involucre number is a reasonable approximation for flower number, since there is relatively little variation in number of flowers per involucre. Involucre from Organ Pipe plants had a mean of 45.69 flowers (s.e. 2.86), while those from Portal plants had a mean of 44.47 flowers (s.e. 2.49). A t-test revealed no significant differences between the population means ($t=0.07$, $df=62$, $p=0.94$).

Statistical analysis of demographic data

Life table estimates and their standard errors were computed for both populations for both years, according to the formulas given by Lee (1980).

Median life expectancies were not estimated for 1985 plants since these were followed only until all surviving individuals had flowered.

To permit comparison of survivorship between spring-flowerers and non-spring-flowerers of the same size, plants were assigned to size classes with at least 20 plants per class. Separate life tables were then computed for each spring-flowering and size-class, for 1986 data and Portal 1985 data.

Because 1985 Organ Pipe plants were marked on different occasions, meaningful size classifications could not be made, but plants could nevertheless be assigned to spring-flowering classes. Life tables were estimated for the entire population and for each spring-flowering class. Separate analyses of the plants marked on each occasion agreed qualitatively with those presented below.

To consider the prediction of greater survivorship among spring-flowerers than non-spring-flowerers of the same size, I tested for survivorship differences among size and spring-flowering classes within each population, using log rank and Wilcoxon rank tests (Lee 1980). Where heterogeneity was shown, pairwise comparisons were performed with Kruskal-Wallis tests (Lee 1980). To compare

frequencies of spring flowerers and survival to summer between years and populations I used a log-linear model.

Since size at onset of flowering can affect both survivorship and fecundity, populations were compared for height at flowering and number of involucre, using oneway analyses of variance (ANOVA). Variation in spring height was further analyzed with twoway ANOVA, using population, spring-flowering class, and their interaction as effects. Similarly, involucre number was further analyzed with a heterogeneity of slopes model (Sokal & Rohlf 1981) using spring height, population, and their interaction as effects. All analyses were conducted on log-transformed data following Kolmogorov-Smirnov tests for normality ($p > 0.01$).

Results

Frequency of Spring Flowering and its Relation to Size

In both years, a smaller proportion of Portal than Organ Pipe plants flowered in spring (table 1.1). Within each population there was little between-year variation in proportion of spring-flowerers (table 1.1). Analysis of a log-linear model for the frequency data showed that the differences among populations in frequency of spring-flowering were highly significant (table 1.2). Within populations, however, differences between years were not significant (table 1.2).

Spring-flowering plants in both populations were significantly larger than non-spring-flowerers (tables 1.1, 1.3). Spring-flowerers at Organ Pipe were significantly smaller than spring-flowerers at Portal (table 1.1). Organ Pipe plants thus tended to flower significantly earlier and at significantly smaller size than Portal plants.

Survivorship

Life table estimates and their standard errors for single-interval mortality, cumulative survivorship, and median life expectancy, are shown in the appendix (tables A1-A4). These life tables describe survivorship in the study populations beginning with the spring marking date, not with germination. Survivorship curves for each size- and spring-flowering class are plotted in figs. 1.2-1.5. Full life tables are given in the Appendix.

At Portal spring-flowering plants are uncommon, making it impossible to classify spring-flowerers by size. The results for Portal (figs. 1.2-1.3) show that spring-flowerers had significantly greater survivorship than did non-spring-flowerers, and that survivorship among the latter increased significantly with size. At Organ Pipe, where spring-flowering is far more common, results (figs. 1.4-1.5) show that the greater survivorship among spring-flowerers holds even among plants of comparable size.

Table 1.2. Analysis of frequencies of spring-flowerers and survival to summer among years and populations. Best-fitting log-linear model.

| <u>Source</u> | <u>df</u> | <u>χ^2</u> | <u>p</u> |
|---------------------------|-----------|----------------------------|----------|
| Population | 1 | 91.88 | 0.0001 |
| Year | 1 | 91.30 | 0.0001 |
| Class ^a | 1 | 529.13 | 0.0001 |
| Surv ^b | 1 | 631.66 | 0.0001 |
| Pop * Year | 1 | 157.05 | 0.0001 |
| Pop * Class | 1 | 321.68 | 0.0001 |
| Pop * Surv | 1 | 140.45 | 0.0001 |
| Class * Surv | 1 | 120.92 | 0.0001 |
| Pop * Year * Surv | 1 | 103.92 | 0.0001 |
| Year * Class * Surv | 1 | 21.96 | 0.0001 |
| Pop * Year * Class * Surv | 1 | 8.01 | 0.0046 |
| Likelihood ratio | 4 | 6.72 | 0.1512 |

Notes:

a: Class = spring-flowerer vs. non-spring-flowerer

b: Surv = survived to summer or did not survive to summer

Table 1.3. Analysis of variance for spring height.

| 1986 Data | | | | |
|------------------|-----------|-----------|----------|----------|
| <u>Source</u> | <u>df</u> | <u>SS</u> | <u>F</u> | <u>p</u> |
| Population | 1 | 1463.16 | 1809.41 | 0.0001 |
| Spring-flowering | | | | |
| class | 1 | 2920.01 | 3611.01 | 0.0001 |
| Pop * class | 1 | 1484.89 | 1836.28 | 0.0001 |
| Error | 2781 | 2246.41 | | |
| 1985 Data | | | | |
| Population | 1 | 122.51 | 86.50 | 0.0001 |
| Spring-flowering | | | | |
| class | 1 | 247.43 | 174.69 | 0.0001 |
| Pop * class | 1 | 39.51 | 127.90 | 0.0001 |
| Error | 577 | 1203.33 | | |

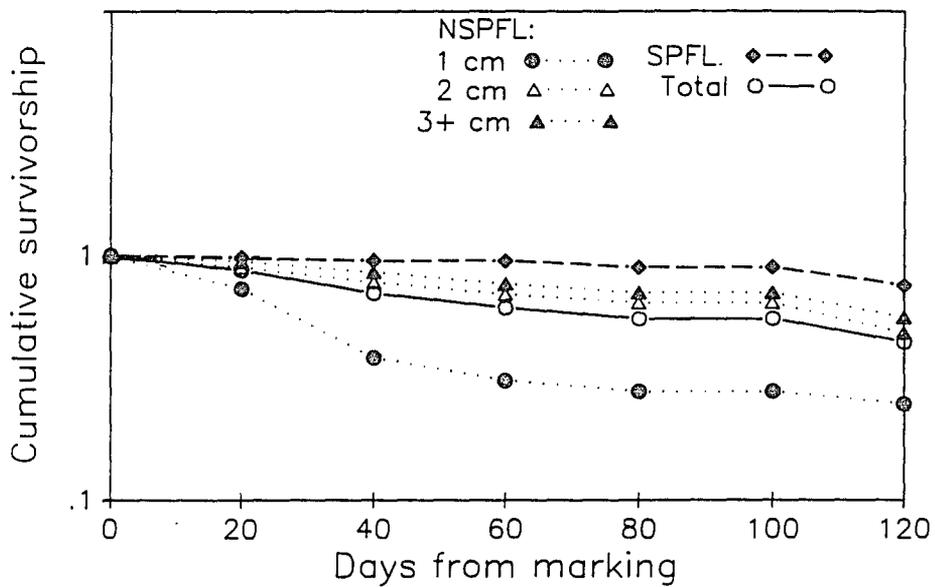


Fig.1.2. Cumulative survivorship for each spring-flowering and size-class, Portal 1985. Tests for equality among classes: logrank, $\chi^2=72.64$, $df=3$, $p<0.0001$; Wilcoxon, $\chi^2=79.67$, $df=3$, $p<0.0001$. {Pairwise Kruskal-Wallis tests: all classes significantly different from others at $p<0.001$, except spring-flowerers and 3+ cm non-spring-flowerers ($p < 0.05$).} SPFL = spring-flowerers, NSPFL = non-spring-flowerers.

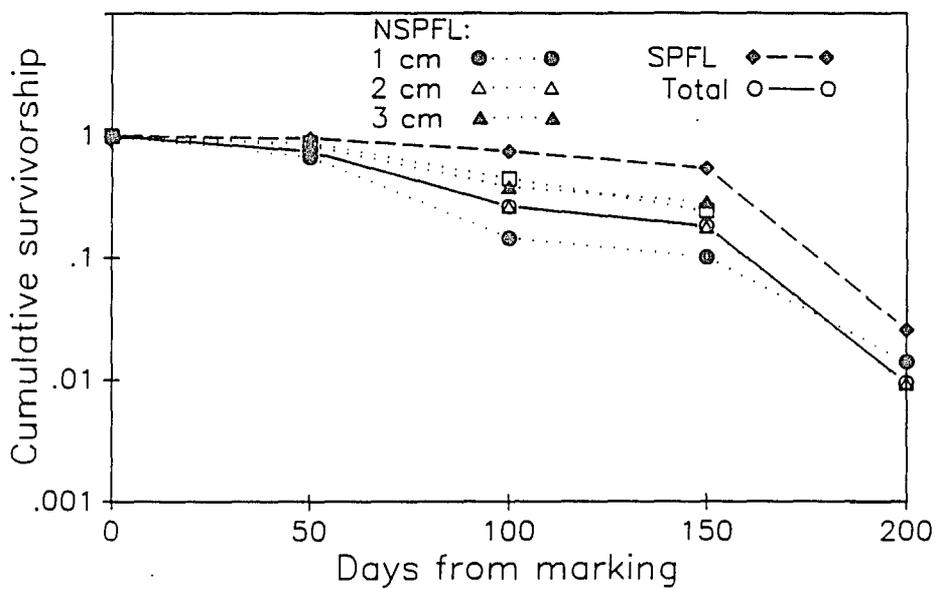


Fig.1.3. Cumulative survivorship for each spring-flowering and size-class, Portal 1986. Tests for equality among classes: logrank, $\chi^2=79.64$, $df=4$, $p<0.0001$; Wilcoxon, $\chi^2=95.79$, $df=1$, $p<0.0001$. (Pairwise Kruskal-Wallis tests: all classes significantly different from others, except no significant difference between 3-cm and 4-cm NSPFL. Significance levels for other comparisons are $p<0.001$, except 4-cm NSPFL with 2-cm and 3-cm NSPFL (both $p<0.01$)). Abbreviations as in fig.1.2.

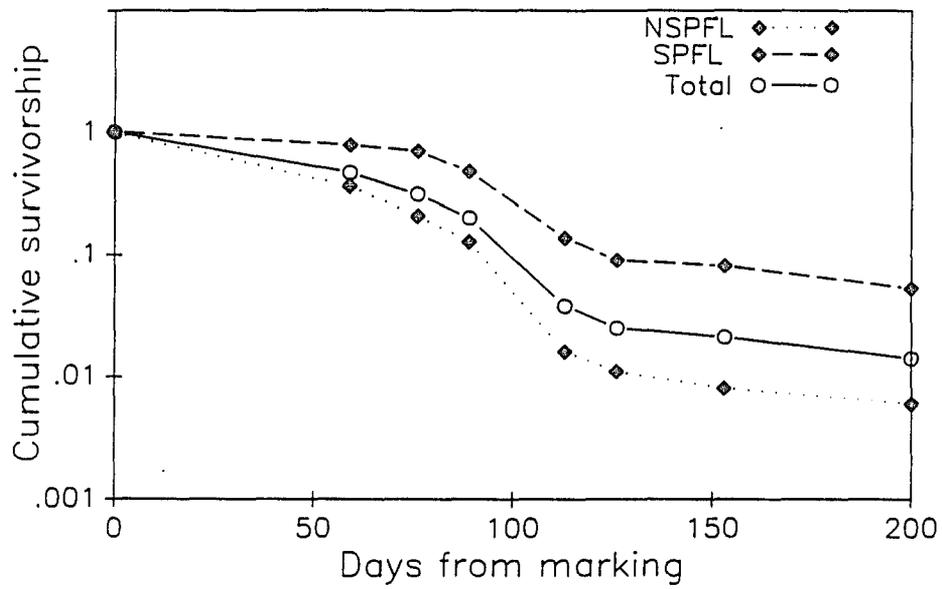


Fig.1.4. Cumulative survivorship for each spring-flowering class, Organ Pipe 1985. Tests for equality among classes: logrank, $\chi^2=29.88$, $df=1$, $p<0.0001$; Wilcoxon, $\chi^2=42.16$, $df=1$, $p<0.0001$. Abbreviations as in fig.1.2.

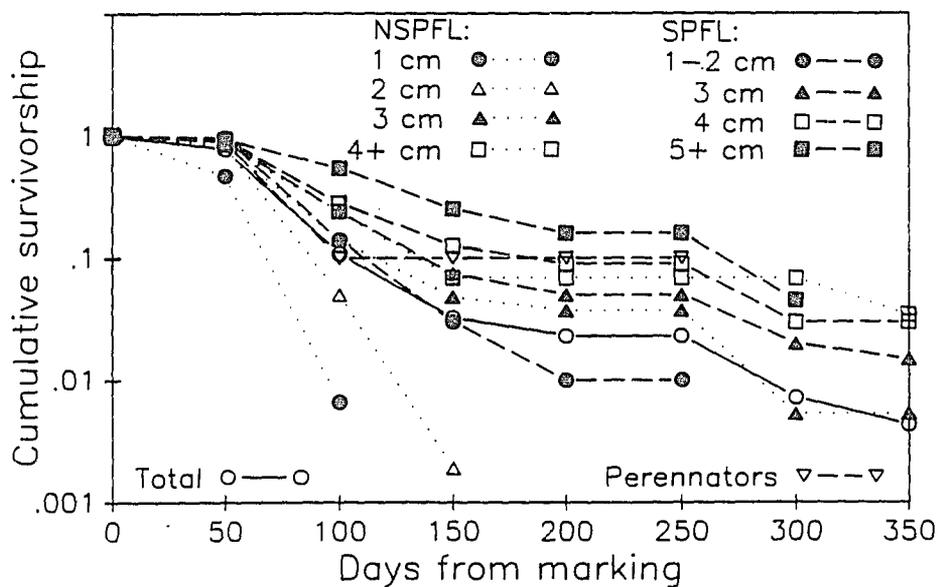


Fig.1.5. Cumulative survivorship for each spring-flowering and size-class, Organ Pipe 1986. Tests for equality among classes: logrank, $\chi^2=422.58$, $df=8$, $p<0.0001$; Wilcoxon, $\chi^2=403.58$, $df=8$, $p<0.0001$. {Pairwise Kruskal-Wallis tests: 1-2 cm SPFL differ from 1-cm NSPFL ($p<0.001$), 2-cm NSPFL ($p<0.001$), 5-10 cm SPFL ($p<0.001$), and 4-cm SPFL ($p<0.01$); 1-cm NSPFL differ from all others ($p<0.001$); 2-cm NSPFL marginally different from perennators ($0.05 < p < 0.10$), and significantly different from all others ($p<0.001$); 3-cm SPFL differ 5-10 cm SPFL ($p<0.001$), and differ marginally from 3-cm NSPFL ($0.05 < p < 0.10$); 3-cm NSPFL differ from 4-cm SPFL ($p<0.01$) and 5-10 cm SPFL ($p<0.001$); 4-6 cm NSPFL differ from 5-10 cm SPFL ($p<0.001$); 4-cm SPFL differ from 5-10 cm SPFL ($p<0.05$) and differ marginally from perennators ($0.05 < p < 0.10$); 5-10 cm SPFL differ from perennators ($p<0.01$).} Other comparisons nonsignificant. Abbreviations as in fig.1.2.

Survival to summer was significantly more common at Portal than at Organ Pipe in both years, as indicated by the significant population * survival term in the log-linear model (table 1.2). The life table analyses (tables A2,A3) suggest that survival to the summer rainy season at Portal was greater in 1985 than in 1986, but between-year differences at Organ Pipe were small. Since the log-linear model showed that populations differed significantly in survival among years, I evaluated chi-square contingency tables for survival x year within each population. These tests revealed that the between-year differences were significant at Portal but nonsignificant at Organ Pipe (Portal $\chi^2=245.73$, $df=1$, $p<0.0001$; Organ Pipe $\chi^2=1.98$, $df=1$, $p=0.159$). In both populations, plants surviving to the summer rainy season had enhanced life expectancies, but this effect was much more marked among Organ Pipe plants (tables A1,A2).

Fecundity

ANOVA showed that mean spring involucre number was greater at Organ Pipe than at Portal in both years (table 1.1). When the comparison was restricted to spring-flowering plants the populations did not differ (table 1.1), indicating that differences in mean spring involucre number were due to the differences in frequency of spring-flowering. Summer involucre number was

significantly greater among Portal plants than among Organ Pipe plants in 1985, but the differences were not significant in 1986 (table 1.1).

In 1986, both spring and summer involucre number were significantly affected by spring height, although the strength of this effect varied between the populations (table 1.4). The 1985 data for spring involucre number did not show a significant effect of size.

Perennation

Perennation is rare at Organ Pipe and appears to be nonexistent at Portal; killing frosts are common at Portal in winter. Only 20 of the 1400 marked plants at Organ Pipe in 1986 had survived from the prior year, as determined by their larger size (5-20 cm to highest node), absence of rosette leaves, and woody stems. None of these plants survived to the summer rainy season in 1986 (table A1). Of the 1380 other plants marked at Organ Pipe in 1986, 13 were still alive after germination had begun in winter 1986-87; none survived to the summer rainy season in 1987. No perennation was observed at Organ Pipe in 1985.

Table 1.4. Relationship of size and fecundity. Heterogeneity of slopes models.

SPRING INVOLUCRES PER SPRING-FLOWERING PLANT, 1986

| Source | df | SS | F | p |
|----------------|-----|-------|--------|--------|
| Spring Height | 1 | 73.23 | 355.47 | 0.0001 |
| Population | 1 | 50.59 | 243.28 | 0.0001 |
| Spg. Ht. * Pop | 1 | 3.35 | 16.12 | 0.0001 |
| Error | 374 | 77.78 | | |

FALL INVOLUCRES PER FALL-FLOWERING PLANT, 1986

| | | | | |
|----------------|-----|-------|-------|--------|
| Spring Height | 1 | 69.48 | 60.46 | 0.0001 |
| Population | 1 | 4.76 | 4.14 | 0.0001 |
| Spg. Ht. * Pop | 1 | 1.97 | 1.71 | 0.0001 |
| Error | 365 | 1.15 | | |

SPRING INVOLUCRES PER SPRING-FLOWERING PLANT, 1985

| | | | | |
|----------------|-----|------|------|--------|
| Spring Height | 1 | 0.00 | 0.15 | 0.6974 |
| Population | 1 | 0.04 | 1.24 | 0.2672 |
| Spg. Ht. * Pop | 1 | 0.00 | 0.00 | 0.9731 |
| Error | 121 | 0.03 | | |

Discussion

Although there is a large literature on life history adaptation in desert annuals (see Introduction and chapter 2 for references), the present study is the first comparison of life history variations among populations of desert annuals. A companion study (chapter 2) is the first consideration of the genetics of desert annual life histories.

Variation among populations

The dramatically lower mean summer rainfall and greater heat at Organ Pipe (fig. 1.1) suggested that selection there would favor a greater proportion of spring-flowerers than at Portal. Data presented here show that the populations differ in the direction predicted. The difference in frequency of spring-flowering is not a result of size differences, since spring-flowering Organ Pipe plants are smaller than their counterparts at Portal (tables 1.1, 1.3). Survivorship to the summer rains, as well as total involucre number, was greater for Portal than for Organ Pipe plants (tables 1.1, A1-A4), indicating a plausible selective basis for the difference in flowering time. Together with greenhouse data demonstrating a genetic basis for these among-population differences (chapter 2), the present

results provide strong support for the adaptive prediction that selection should favor earlier flowering in Sonoran desert populations.

Variation within populations

Onset of flowering in individual plants appears to be strongly influenced by environmental factors. In the greenhouse, flowering was significantly delayed by single, severe drought events, as well as by reduction in frequency of watering (chapter 2). These experimental results suggested that spring-flowering plants in the field may enjoy not only a size, but also a water status advantage.

The present results confirm this prediction: spring-flowering plants have improved survivorship probabilities even when size is held constant (figs. 1.2 - 1.5); they also have enhanced fecundity. In 1986 there were significant positive Spearman rank correlations among spring-flowerers between spring involucre number and summer involucre number (Organ Pipe $R=0.50$, $p=0.0007$; Portal $R=0.31$, $p=0.0001$), and among all plants between spring involucre number and date of death: (Organ Pipe $R=0.34$, $p<0.0001$; Portal $R=0.15$, $p<0.0001$).

Evaluation of the Model

The results show that spring-flowering is more prevalent at Organ Pipe, as expected. Since this variation appears to have a genetic basis (chapter 2), the

present case is an interesting test of a simple optimization model. Clearly *E. abertianum* plants flower in both spring and summer in both location studied (tables A1-A4). Is summer fecundity sufficient to offset the risk of additional mortality during the foresummer drought?

For Portal plants, substitution from the field data (table 1.1) into eq. (2) gives

$$g_2/g_1 > (s_{11} - .03)/69.97 \quad (4a)$$

for 1985, and

$$g_2/g_1 > (s_{11} - .03)/4.62 \quad (4b)$$

for 1986. Conditions (4a-4b) favoring a spring-plus-summer life history hold regardless of relative seed survivorship so long as s_{11} -- the average fecundity of a spring-only plant -- is less than 70 for 1985 and less than 4.65 for 1986. Since the measured mean spring fecundity in both years was 0.03 (table 1.1), spring-only plants would be favored only if their average spring fecundity increased at least 2333-fold in 1985, and at least 155-fold in 1986. These are minimum estimates: differences in seed survivorship would require even greater fecundity increases by spring-only plants.

For Organ Pipe plants, analogous substitutions give

$$g_2/g_1 > (s_{11} - .21)/.07 \quad (4c)$$

for 1985, and

$$g_2/g_1 > (s_{11} - .67)/.498 \quad (4d)$$

for 1986. Conditions (4c-4d) favoring a spring-plus-summer life history hold without differential seed survivorship only for s_{11} less than .28 in 1985 and for s_{11} less than 1.17 in 1986. For spring-plus-summer plants to retain an advantage, increases in average spring fecundity as small as 1.3-fold for 1985 and 1.74-fold for 1986 would require differential seed survivorship. Since these increases seem within the range of possibility, it is useful to consider values for relative seed survivorship and spring fecundity for which (4c-4d) hold. Solutions satisfying (4c-4d) are shown by the shaded region in fig. 1.6. These results indicate that unless survivorship of spring seeds is extremely low compared with that of summer seeds ($g_2 \gg g_1$), small increases in spring fecundity would favor a spring-only syndrome in the years studied.

This analysis suggests that at Portal the high-variance (spring-plus-summer) phenology appears to be associated with a high mean: the fecundity differential necessary to favor a spring-only syndrome appears to be extreme in the years studied. However, at Organ Pipe the advantage of spring-plus-summer plants in the years studied is marginal at best. In both 1985 and 1986, small increases in average spring fecundity would favor a spring-only habit, unless the relative survivorship of spring seeds is quite small (fig. 1.6).

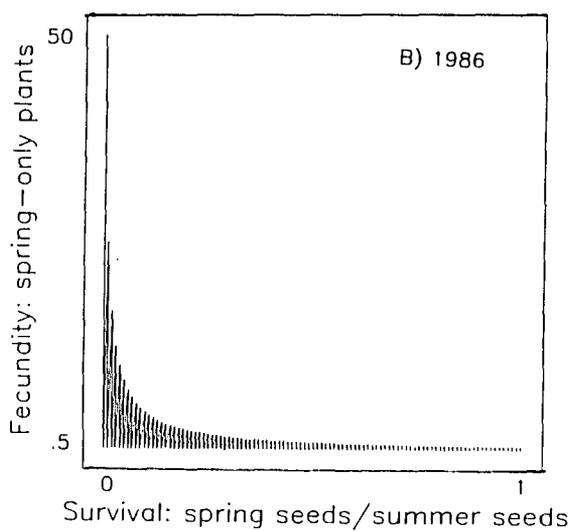
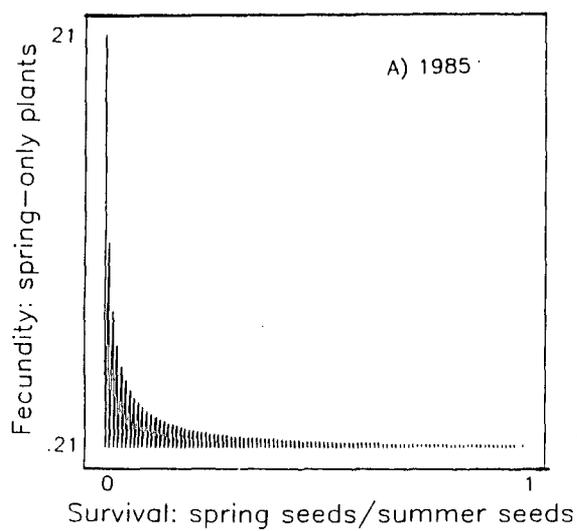


Fig.1.6. Values of relative seed survivorship and of fecundity for a spring-only plant which favor a spring-plus-summer life history at Organ Pipe: a) 1985; b) 1986.

The comparison of spring-plus-summer with spring-only life histories is interesting because the spring-only habit is more common among winter-germinating desert annuals (chapter 2); however, a summer-only habit could also be possible. Unfortunately it is difficult to consider an analog to eq. (1) comparing spring-plus-summer with summer-only habits, since there is no *a priori* reason to expect one or the other habit to have greater variance. Put simply, this is because plants of both types would live for the same period; their relative fitness variances would therefore depend on how variance in survival to and fecundity in summer is affected by flowering in spring. There are no data with which to address this issue.

Perennation appears not to be a viable alternative at Portal because of killing frosts. Perennation does occur in some years at Organ Pipe, but is rare. Perennating individuals produced very few additional flowers in their second year (chapter 3). A greenhouse study showed that offspring of perennating plants lived longer than offspring of a random population sample, but the two groups did not differ significantly in total involucre production (chapter 3).

Adaptive and historical explanations

The earlier time of flowering at Organ Pipe appears to be adaptive. Greenhouse studies (chapter 2) have shown a genetic basis for among-population differences in these traits, and the present results (tables 1.1 ,A1,A2) show that delayed flowering at Organ Pipe has dire fitness consequences. Other Sonoran Desert populations of *E. abertianum* also have large proportions of spring-flowering plants (chapter 2).

Data from Organ Pipe, but not from Portal, suggest that the fecundity gained in the summer may not offset the risk of mortality during the severe foresummer drought. Because these data are for only two years in a notoriously variable environment, this result requires cautious interpretation.

Evidence for each site suggests that the present results do not represent extremes for either population. For the Portal site, I derived survivorship estimates from unpublished data provided by D.A. Samson, T.E. Philippi, and D.W. Davidson (table 1.5). These workers and their associates made counts of individual plants in study plots at Portal were made in April and September of each year from 1978 to 1987. As these counts were part of an ongoing manipulative experiment, I used data only from unmanipulated control plots. The percentage of surviving plants and its standard error are given for each year in table 1.5. These data show considerable variation around a mean of 16%

survival from April to September. Survivorship estimates from the data of Samson et al. differ somewhat from those in the present study because their study used different areas of this large study site, and because their sampling occurred over a different time interval. While these differences dictate caution in comparing data sets, survivorship during the present study appears to have been within the normal range of variation for this site.

Distributional data for the Organ Pipe region also suggests that the present results may be fairly general. *E. abertianum* is absent from the low-summer-rainfall region immediately west of the Ajo Mts., an area in which it is clearly unlikely for the spring-plus-summer habit to be favored. Rather than observing an adaptive switch from spring-plus-summer to spring-only phenologies somewhere near the Ajo Mts., we observe a spring-plus-summer phenology up to and including this mountain range, and the complete absence of the species to the west. The distributional data thus provide important support for the conclusion that life history evolution in this species, at least at Organ Pipe, is not adequately described by eq. (1).

Our understanding of life history evolution in *E. abertianum* can be greatly improved with the addition of information on the probable ancestral state of this species. Systematic studies of *Eriogonum*, subgenus *Ganysma*, have suggested a Mexican origin for the major species groups, and northward

Table 1.5. Additional estimates of Portal survivorship 1978-1987.

| <u>Year</u> | <u>N</u> | <u>Survival (s.e.)</u> <u>April - Sept.</u> |
|-------------|----------|--|
| 1978 | 2345 | 0.019 (0.003) |
| 1979 | 346 | 0.691 (0.024) |
| 1981 | 1290 | 0.150 (0.010) |
| 1982 | 2099 | 0.062 (0.005) |
| 1983 | 1282 | 0.218 (0.012) |
| 1984 | 75 | 0.067 (0.029) |
| 1985 | 83 | 0.169 (0.041) |
| 1986 | 188 | 0.048 (0.016) |
| 1987 | 723 | 0.058 (0.009) |

Source: D.A. Samson, T.E. Phillipi, D.W. Davidson, unpubl. data.

Data for 1980 unavailable.

migrations with the end of glacial periods (Reveal 1969). Based on its current distribution (cent. s. Arizona and New Mexico, and w. Texas, s. into Sonora, Chihuahua, and Coahuila, s. to San Luis Potosì; Reveal 1976), *E. abertianum* probably originated in or around the Chihuahuan Desert. Rainfall in the Chihuahuan Desert occurs mainly in the summer, and winter temperatures are generally cooler in the Chihuahuan Desert than in the Sonoran Desert; few *E. abertianum* flower in spring in the Chihuahuan desert (table 1.1; chapter 2). It is therefore likely that the ancestral *E. abertianum* populations were largely summer-flowering plants.

This conclusion marches well with fossil evidence indicating that *E. abertianum* invaded the Sonoran desert during a period in which summers were substantially cooler and wetter than the present -- i.e., a period in which summers were roughly similar to those in today's Chihuahuan Desert (T.R. Van Devender, pers. comm.). The earliest fossil *E. abertianum* found in Sonoran Desert packrat middens are from the period of transition between woodland and desert scrub plant communities (Van Devender 1977), 8260 ± 130 yr B.P. (radiocarbon no. A-4780; T.R. Van Devender, pers. comm.). At Organ Pipe the earliest fossil *E. abertianum*, found < 5 km from the present study site, dates from 1150 ± 240 yr B.P. The Organ Pipe climate at that time was clearly wetter than the present: fossil packrat middens of the same period from south-facing

slopes in the nearby Puerto Blanco Mts. (9 km SW from the Ajo Mt. site) include a number of species currently restricted to riparian areas (Van Devender 1987).

If the ancestral *E. abertianum* populations were mainly summer-flowering, the among-population differences in the present study seem likely to be consequences of adaptation in Sonoran Desert populations. This interpretation is reinforced by greenhouse studies indicating a genetic basis for this among-population variation (chapter 2). But climatic change in the Sonoran Desert appears to have occurred more rapidly than adaptation in *E. abertianum* populations. In addition to the present Organ Pipe data suggesting that average summer fecundity may not outweigh the risk of foresummer mortality, this view is supported by fossil evidence. In the Waterman Mts. (ca. 50 km NW of Tucson), *E. abertianum* is presently not found below 914 m elevation, and there only on a single north-facing slope (pers.obs.; T.R. Van Devender and T. Burgess, pers. comms.), but 8260 \pm 130 yr B.P. and 5540 \pm 70 yr B.P. fossils have been found on south-facing slopes at 792 m (radiocarbon nos. A-4780 and A-4781, respectively).

The fossil and biogeographic data thus provide additional support for the hypothesis that the earlier time of flowering among Organ Pipe plants is likely to be a consequence of natural selection. However, these data also suggest that

adaptation may not have kept pace with climatic change. When these data are considered jointly with the phylogenetic, demographic, and distributional data, it becomes difficult to escape the conclusion that factors other than simple fitness maximization have played important roles in the evolution of life histories in *E. abertianum* populations.

Can the apparent fit of eq. (1) to the Portal data be interpreted as evidence for natural selection in this population? Such a view seems questionable. The spring-plus-summer phenology seen in these plants appears likely to be an ancestral character which has been modified in Sonoran Desert populations to a limited extent. Concordance between the predictions of optimization models and data can only imply that a trait has positive fitness consequences, not that the trait is necessarily a consequence of natural selection. In the terminology of Gould and Vrba (1982), such traits may be "aptations" rather than "adaptations." Distinguishing between these alternatives -- which may not always be possible -- is likely to require historical information. In the present case the historical data do not suggest an adaptive origin of the spring-plus-summer phenology at Portal.

The invariance of the spring-plus-summer habit is not explained by the demographic, distributional, fossil, or genetic (chapter 2) data. Since the spring-plus-summer habit is shared by virtually all annuals in this genus, it might be

tempting to join several recent authors (e.g., Cheverud et al. 1985; Clutton-Brock and Harvey 1977, 1979, 1980) in characterizing such cases as examples of "phylogenetic constraint." But it is not clear how natural selection might be constrained by phylogeny other than through the inheritance of particular developmental pathways or the particular genetic architecture of selected traits. It seems more useful to ask what particular developmental or genetic factors limit variation. Our further understanding of life history evolution may depend partly on our ability to give material content to such concepts as "constraints" and "taxonomic biases" (Stearns 1980, 1983, 1984, 1985).

CHAPTER TWO

Adaptive and Non-Adaptive Explanations for Variable Flowering

Introduction

The prevalence of annual plants in hot deserts, and their physiological similarities, are frequently considered evidence of the adaptive evolution of life histories (e.g., Gleason & Cronquist 1964, Schaffer & Gadgil 1975, Mulroy & Rundel 1977, Orians & Solbrig 1977a, Silvertown 1982). Desert annuals show many traits predicted by models of optimal life histories (e.g., Schaffer & Gadgil 1975), such as prodigious photosynthetic rates (Seaman et al. 1979, Werk et al. 1983, Ehleringer 1985) and drought-resistant seeds resulting in substantial seed banks (Whitson 1975, 1976; Price & Reichmann 1987). There is often predictable variation in temperature-sensitivity of germination, photosynthetic pathway, and morphology, depending on the season in which the plants are active (Went 1949, Mulroy & Rundel 1977). This adaptive view of desert annual life histories is especially persuasive because these features are repeated among unrelated taxa in hot deserts around the world (Orians & Solbrig 1977b, Gutterman 1982), and because most desert annual species are relatively recently derived (Johnson 1968, Axelrod 1979).

In view of this comparative evidence for adaptation, can we expect to explain many of the details of desert annual life histories in terms of natural selection? Much of modern evolutionary biology has consisted of such efforts to

explain among- and within-population variability in terms of their adaptive significance, and to infer thereby the role of natural selection (c.f., Mayr 1983). However, there are several difficulties with this approach. Not least among these is the problem of distinguishing between the consequences of selection and the consequences of invariant physiological or developmental mechanisms, lack of appropriate genetic variation, or drift (Gould & Lewontin 1979). It seems reasonable to speculate that such distinctions may tend to become more difficult as one moves from broad comparative studies to the details of population-level variability.

The experiments discussed here concern variation in time and size at flowering in the desert annual *Eriogonum abertianum* Torr. (Polygonaceae). Populations vary in the direction predicted from an adaptive perspective, and I show below that this variation has a strong genetic component. However, I also show that lack of moisture delays flowering in this species, suggesting that much of the phenological complexity within wild populations (fig. 2.1, chapter 1) may be a simple consequence of seasonal drought. This conclusion is strengthened by evidence that flowering is delayed by lack of moisture in virtually all herbaceous annuals studied. This comparative and experimental evidence thus points to the unexpected conclusion that the widespread claim of drought-induced flowering in desert annuals (Leopold & Kriedemann 1975, Cohen 1976, Solbrig et al. 1977, Rathcke & Lacey 1985, Lacey 1986) lacks empirical support.

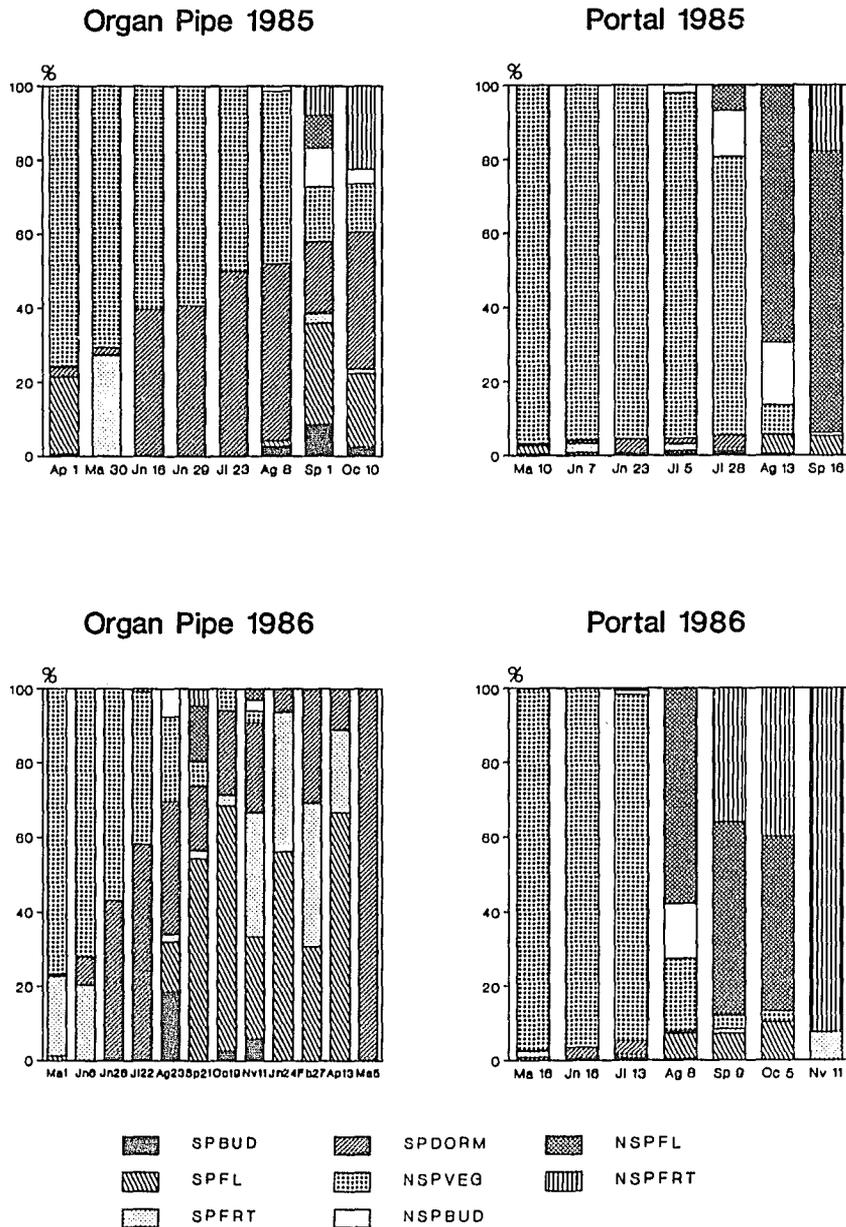


Fig. 2.1 Distribution of phenologic stages in two populations of *E. abertianum*. Prefixes: 'SP'= spring flowerer, 'NSP'= non-spring-flowerer. Suffixes: 'BUD'=budding, 'FL' = flowering, 'FRT'= fruiting, no flowers, 'DORM' = no longer reproductive, 'VEG' = prereproductive.

Study species and hypotheses

The widely used categories "winter" and "summer" annuals (Shreve 1951, Mulroy & Rundel 1977), cannot be applied meaningfully to *E. abertianum*. As with most annual erigonums, there are two fairly distinct flowering periods, late spring and late summer -early fall (Reveal 1968, Davidson 1977, Inouye 1980, chapter 1). Individuals which flower in the spring resume flowering after the onset of summer monsoon rains, while other individuals flower for the first time in the summer (fig. 2.1). Germination, however, occurs exclusively in response to winter rains (Christou 1974; Whitson 1975, 1976; Davidson 1977; Inouye 1980; Davidson et al. 1985).

Reproduction requires continued growth in *E. abertianum* because the development of flowers and related structures depends anatomically on shoot elongation. Flowers occur within involucre, which are produced at each node after onset of flowering (fig. 2.2). Extensive indeterminate branching begins at the first involucre-bearing node, so the number of involucres increases rapidly with continued growth. Total fecundity is linked to continued growth because 1) flowering proceeds from the bottom of the plant towards the top; 2) once flowering begins at a node, additional involucres are not produced there unless tissue above that node is removed; and 3) flowers are produced within an

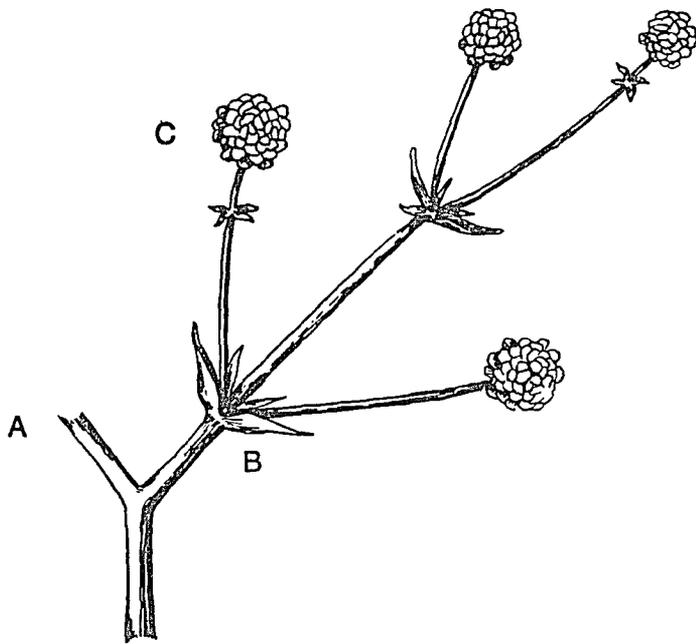


Fig. 2.2. Inflorescence of *E. abertianum*. A) Indeterminate branch. B) Node with reproductive structures. C) Involucre containing flowers.

involucre for only about 3 wk (pers. obs.). Lindenmayer (1984) reaches the same conclusion in discussing this kind of branching pattern in an inflorescence.

This species originated in or near the Chihuahuan Desert, and invaded the Sonoran Desert during a cooler, wetter period than the present, as indicated by fossil and biogeographic evidence (chapter 1). Today the proportion of spring-flowering plants in wild populations of *E. abertianum* is greater at Sonoran than Chihuahuan Desert sites (fig. 2.1, table 2.1; chapter 1). As one might expect, the shift in flowering time is accompanied by a reduction in size at onset of flowering (table 2.1; chapter 1). The possibility of an adaptive origin for this shift in flowering time is suggested not only by the substantially hotter, drier, and less predictable climate of the Sonoran Desert, but also by the profound demographic consequences of flowering time in wild populations (chapter 1). I test below the hypothesis that there is a genetic basis for this among-population variation.

There are fewer reasons to suspect an adaptive origin for the multiple flowering episodes within individuals, or for the bimodality in onset of flowering within populations. Spring-flowering plants have both survivorship and fecundity advantages as compared with non-spring-flowerers (chapter 1), making the persistence of a non-spring-flowering "strategy" difficult to explain under an adaptive scenario. To make matters worse, summer-fall fecundity does not necessarily offset the risk of mortality during the interval between flowering

Table 2.1. Frequencies and sizes of spring-flowering classes of *E. abertianum* in several populations.

| Site & Date | % Spring Plants | | Mean (s.e.) Ht. to Highest Node (cm) | | | |
|-------------------|--------------------|--------------------|--------------------------------------|------|--|--|
| | Flowered* | Which Flowerers | Non-Flowerers | N | | |
| CHIHUAHUAN DESERT | | | | | | |
| Portal | | | | | | |
| 5/10/85 | 2.6 | 4.4 (.58) | 2.2 (.05) | 494 | | |
| 5/16/86 | 2.6 | 4.8 (.43) | 1.7 (.03) | 1404 | | |
| Sierra Vista | | | | | | |
| 5/31/86 | 0.0 | --- | 1.3 (.04) | 200 | | |
| SONORAN DESERT | | | | | | |
| Tucson Mts. | | | | | | |
| 6/6/86 | 56.7 | 2.8 (.10) | 1.7 (.06) | 201 | | |
| Waterman Mts. | | | | | | |
| 5/20/86 | 31.0 | 4.2 (.43) | 2.0 (.05) | 200 | | |
| Organ Pipe | | | | | | |
| 4/1/85 | 21.3 | 2.5 (.19) | 1.5 (.06) | 150 | | |
| 5/10/86 | 23.1 | 3.1 (.07) | 1.7 (.02) | 1382 | | |

* Chisquare tests for heterogeneity were significant at $p < .05$ for 1986 sample as a whole as well as for all pairwise comparisons.

seasons (chapter 1). Finally, multiple flowering seasons within populations and multiple flowering episodes within individuals appear to be the rule among annuals in this genus (Reveal 1968). Because reproduction is necessarily coupled with growth in this species, the bimodality in flowering activity may simply result from seasonal drought. I test below the hypothesis that drought directly inhibits onset of flowering in *E. abertianum*.

If the underlying developmental pattern of this species constrains its reproductive biology in the manner suggested above, two secondary hypotheses suggest themselves. First, responses to drought should not vary among populations or families. Second, within populations there should be a positive genetic correlation between fecundity and length of reproductive period. These hypotheses are also considered below.

Materials and Methods

Study populations were located at a Chihuahuan Desert site on the lower Cave Creek bajada of the Chiricahua Mts. near Portal, Arizona, and at a Sonoran Desert site on a rocky south-facing slope in the Ajo Mountains at Organ Pipe Cactus National Monument (see chapter 1 for climatic descriptions). The Organ Pipe site is < 5 km from an 1150 ± 240 yr B.P. fossil packrat midden containing *E. abertianum* (Alamo Canyon site, radiocarbon no. A-2121;

T.R. Van Devender, pers. comm.), suggesting that the Organ Pipe populations are quite old.

Drought experiment: design

To examine the effects of population of origin and drought on the size and time at onset of reproduction, plants were exposed to simulated droughts of varied length and starting date. Seeds were collected at both sites in October 1984. In February 1985 they were planted on clean sand in pots in the greenhouse, and misted daily until cotyledons emerged. On emergence all but the seedling closest to the center of the pot were removed. Plants were watered weekly to field capacity, except during drought treatments. The experiment was an unbalanced factorial design, varying drought length (zero, two, four, or six weeks), drought starting date (three dates separated by two-week intervals), and population. Thus for each population there were ten cells of 30 plants each, or a total of 600 plants. Plants were positioned randomly on greenhouse benches, and assigned randomly to treatment groups. Time until first flower bud and height to highest node at that time were measured. Plants were followed until budding; date of death was recorded for plants dying before budding. The greenhouse was neither heated nor cooled during this experiment.

Watering experiment: design

To examine the extent of genetic variation within and among populations, as well as to consider the effect of variations in regular watering regimes, maternal sibships from each population were exposed to either weekly or nonweekly watering. Seeds were collected from 40 plants at each site in October 1985. In February 1986 they were planted in the greenhouse in pots filled with clean sand, covered with vermiculite, and misted daily until cotyledons emerged. Seedlings were thinned as above. For each family, 3 pots received weekly, and 3 biweekly, watering treatments. Treatment began at formation of the first leaf (hereafter "establishment") for each plant. Plants were positioned randomly on greenhouse benches. Leaf number and height to highest node were recorded at time of first bud and at anthesis. Time until emergence, establishment, first flower bud, anthesis, last flowering, and death, and involucre number at cessation of flowering, were recorded for all plants. All plants were followed until death. From mid-May to late September an evaporative cooler operated continuously in the greenhouse.

Statistical analyses: drought and watering experiments

1) **Event time data.** Variables defined as "time until an event occurs" were analyzed using accelerated failure time models. These models assume only that a baseline distribution of failure times is modified ("accelerated") by a regression

of failure times on covariates. Fitting the model thus involves estimating shape and scale parameters for the baseline distribution, as well as regression parameters for the covariates. These models have been widely used in medicine and industry, and were recently introduced into the ecological literature by Muncheow (1986) and Pyke and Thompson (1986), who provide readily accessible introductions to their uses and interpretation. More rigorous discussions can be found in Lee (1980) and Lawless (1982). Routines for evaluating these models are available in two widely used statistical packages (SAS and BMDP), and Lee (1980) provides FORTRAN code for the same purpose.

Failure time models offer several advantages over analyses of variance (ANOVA) for event time data. Such data are often "right-censored:" the study ends or death or other loss to follow-up occurs before a response is recorded for some individuals. Because distributions (not means) of failure times are analyzed with these models, right-censored data points can be used to estimate the probability of failure up to the censorship time. ANOVA must treat such data as missing -- potentially biasing the results in the present case, because drought and watering treatments can increase mortality. Additionally, event time data are frequently not normally distributed, but failure time models can be used with arbitrary distributions. An additional advantage is that these models allow one to

compare distributions rather than means, by comparing shape and scale parameters.

To determine the effect of population and of treatments on event times, population and treatment groups were analyzed as covariates for both experiments. Population x treatment interactions and emergence time were also analyzed as covariates for the watering experiment. It was not possible to analyze models using some covariates (families within populations in the watering experiment, and population x treatment interactions in the drought experiment), because the model equations do not have unique solutions if all points in one or more cells are right-censored. Significance of each regression parameter was evaluated with loglikelihood tests (Lee 1980, Lawless 1982). Frequency of survival until flowering was compared among populations and treatments in each experiment with chi-square tests. Gamma distributions -- the most general of those commonly used for failure time models -- were used for all analyses because there were no *a priori* reasons to expect results to fit any particular distribution.

2) Size and fecundity data. Variables related to fecundity and size were analyzed with ANOVA. Data were transformed to achieve normality. SAS Type IV sums of squares were used in the analyses, because there were empty cells (Freund et al. 1986). Population, family, and all interactions including these terms were considered random in the watering experiment. As with most

unbalanced ANOVAs including random terms, it was necessary to use approximate F-tests (Milliken & Johnson 1984). Emergence time was considered a block effect.

3) Genetic correlation. Because few traits were normally distributed, it was impossible to estimate the components of genetic variance and covariance necessary to compute genetic correlations *sensu strictu*. Instead I calculated correlations among family means within each population for each trait in the watering experiment. Correlations among size traits were calculated as Pearson product-moment correlations weighted by family size. Correlations involving event time traits were calculated as Spearman rank correlations, because trait values were not normally distributed.

4) Reporting of correlated variables. Exploratory data analyses revealed that all size variables were positively correlated ($p < 0.0001$) and that time to first bud and time to anthesis were also positively correlated ($p < 0.0001$). Consequently I report below analyses only for time to first bud and height at that time; analyses of the other correlated variables yielded nearly identical results.

Parents and Offspring: design

To examine the genetic basis of flowering time and size independently from the watering experiment, seeds produced in the drought experiment were

planted at the same time and manner as in the watering experiment. Four offspring were grown from each of 40 maternal plants from each population. Plants were watered weekly. Time and height at first flower bud and at anthesis, as well as involucre number, were recorded.

Parents and offspring: statistical analysis

The resemblance between parent and offspring was examined by regression of mean offspring height at first bud on maternal parent height at time of first flower bud. Offspring means were weighted by family size. Spearman rank correlations rather than regressions were used to analyze the relationship between offspring mean and maternal parent time to first bud, because these data were not normally distributed. As above, exploratory data analyses revealed positive correlations ($p < 0.0001$) between both the size and the time variables; results reported below are therefore restricted to time to first bud and height at that time.

Intraclass correlations

Heritability can be directly computed from either parent-offspring regressions, if the relatedness of sibs is known and if one can assume that no environmental correlations or epistasis exist (Bulmer 1985). Unfortunately the mating system of *E. abertianum* is unknown, so heritabilities cannot be

computed. However, intraclass correlations can be estimated from both the watering and parent-offspring experiments, providing independent qualitative tests of the existence of genetic variation for traits of interest. Heritabilities could also be calculated from intraclass correlations.

Variance components for size traits and involucre number were estimated from the watering experiment and from the F_2 generation in the parent-offspring experiment. These estimates were used to calculate the intraclass correlation coefficient

$$t = s_b^2 / (s_b^2 + s_w^2) \quad (1)$$

where s_b^2 and s_w^2 are variance among and within classes, respectively (Bulmer 1985). Because data were unbalanced, restricted maximum likelihood estimators for variance components were used (Milliken & Johnson 1984; Shaw 1987). Values of t were calculated for both among- and within-population variances.

Results

Timing of life history events

Organ Pipe plants began budding earlier than Portal plants in both the watering and drought experiments, as revealed by failure time analyses (table 2.2). To interpret tables 2.2 - 2.3, recall that this approach involves estimation of the baseline distribution of failure times (i.e., the scale and shape parameters for the gamma distribution) as well as the manner in which these failure times are

Table 2.2. Failure time analyses for time to first bud.

| Variable | df | Regression | | |
|-----------------------------------|----|------------------|----------|--------|
| | | Parameter (s.e.) | χ^2 | p |
| DROUGHT EXPERIMENT | | | | |
| Intercept | 1 | 2.447 (0.051) | 2305.73 | 0.0001 |
| Population, Organ Pipe | 1 | -0.134 (0.028) | 23.92 | 0.0001 |
| Portal | 0 | 0.000 | | |
| Drought length, total | 3 | | 48.48 | 0.0001 |
| 0 wks. | 1 | -0.304 (0.053) | 32.97 | 0.0001 |
| 2 wks. | 1 | -0.203 (0.048) | 17.72 | 0.0001 |
| 4 wks. | 0 | 0.000 | | |
| 6 wks. | 1 | 0.003 (0.610) | 0.00 | 0.9549 |
| Drought start, total | 2 | | 25.32 | 0.0001 |
| control | 0 | 0.000 | | |
| May 14 | 0 | 0.000 | | |
| May 28 | 1 | 0.056 (0.034) | 2.60 | 0.1070 |
| June 11 | 1 | 0.194 (0.039) | 24.18 | 0.0001 |
| Gamma scale parameter | 1 | 0.156 (0.012) | | |
| Gamma shape parameter | 1 | 1.788 (0.197) | | |
| Maximized loglikelihood = -163.16 | | | | |

Table 2.2, contd.

| Variable | df | Regression | | |
|---------------------------------|----|------------------|----------|--------|
| | | Parameter (s.e.) | χ^2 | p |
| WATERING EXPERIMENT | | | | |
| Intercept | 1 | 4.408 (0.025) | 30539.80 | 0.0001 |
| Emergence date | 1 | 0.005 (0.001) | 23.99 | 0.0001 |
| Population, total | 1 | | 272.61 | 0.0001 |
| Organ Pipe | 1 | -0.480 (0.029) | 272.61 | 0.0001 |
| Portal | 0 | 0.000 | | |
| Treatment, total | 1 | | 6.94 | 0.0084 |
| weekly | 1 | -0.068 (0.026) | 6.94 | 0.0084 |
| biweekly | 0 | 0.000 | | |
| Pop * treat, total | 1 | | 0.57 | 0.4493 |
| Organ Pipe, weekly | 1 | 0.031 (0.041) | 0.57 | 0.4493 |
| Organ Pipe, biweekly | 0 | 0.000 | | |
| Portal, weekly | 0 | 0.000 | | |
| Portal, biweekly | 0 | 0.000 | | |
| Gamma scale parameter | 1 | 0.133 (0.011) | | |
| Gamma shape parameter | 1 | -1.527 (0.219) | | |
| Maximized loglikelihood = 44.68 | | | | |

Table 2.3. Failure time analyses for time to establishment, last flower, and death, in watering experiment.

| Variable | df | Regression | | |
|---------------------------------|----|------------------|----------|--------|
| | | Parameter (s.e.) | χ^2 | p |
| TIME TO ESTABLISHMENT | | | | |
| Intercept | 1 | 4.3490 (0.0246) | 31207.80 | 0.0001 |
| Population, total | 1 | | 139.02 | 0.0001 |
| Organ Pipe | 1 | -0.3767 (0.0319) | 139.02 | 0.0001 |
| Portal | 0 | 0.0000 | | |
| Gamma scale parameter | 1 | 0.2040 (0.0120) | | |
| Gamma shape parameter | 1 | -0.6059 (0.1370) | | |
| Maximized loglikelihood = 19.04 | | | | |

Table 2.3, cont'd.

| Variable | df | Regression | | |
|---------------------------------|----|------------------|----------|--------|
| | | Parameter (s.e.) | χ^2 | p |
| TIME TO LAST FLOWER | | | | |
| Intercept | 1 | 5.3518 (0.0239) | 50211.40 | 0.0001 |
| Emergence date | 1 | 0.0002 (0.0009) | 0.08 | 0.7744 |
| Population, total | 1 | | 16.56 | 0.0001 |
| Organ Pipe | 1 | 0.1428 (0.0351) | 16.56 | 0.0001 |
| Portal | 0 | 0.0000 | | |
| Treatment, total | 1 | | 0.51 | 0.4764 |
| weekly | 1 | 0.0150 (0.0210) | 0.51 | 0.4764 |
| biweekly | 0 | 0.0000 | | |
| Pop*treat, total | 1 | | 0.96 | 0.3267 |
| Organ Pipe, weekly | 1 | 0.0359 (0.0366) | 0.96 | 0.3267 |
| Organ Pipe, biweekly | 0 | 0.0000 | | |
| Portal, weekly | 0 | 0.0000 | | |
| Portal, biweekly | 0 | 0.0000 | | |
| Gamma scale parameter | 1 | 0.1073 (0.0107) | | |
| Gamma shape parameter | 1 | 2.1472 (0.4905) | | |
| Maximized loglikelihood = 48.99 | | | | |

Table 2.3, cont'd.

| Variable | df | Regression | | |
|-----------------------------------|----|------------------|----------|--------|
| | | Parameter (s.e.) | χ^2 | p |
| TIME TO DEATH | | | | |
| Intercept | 1 | 5.6100 (0.0244) | 52660.40 | 0.0001 |
| Emergence date | 1 | 0.0003 (0.0012) | 0.06 | 0.8038 |
| Population, total | 1 | | 0.19 | 0.6594 |
| Organ Pipe | 1 | 0.0076 (0.0174) | 0.19 | 0.6594 |
| Portal | 0 | 0.0000 | | |
| Treatment, total | 1 | | 0.05 | 0.8183 |
| weekly | 1 | -0.0048 (0.0209) | 0.05 | 0.8183 |
| biweekly | 0 | 0.0000 | | |
| Pop*treat, total | 1 | | 0.36 | 0.5505 |
| Organ Pipe, weekly | 1 | 0.0155 (0.0260) | 0.36 | 0.5505 |
| Organ Pipe, biweekly | 0 | 0.0000 | | |
| Portal, weekly | 0 | 0.0000 | | |
| Portal, biweekly | 0 | 0.0000 | | |
| Gamma scale parameter | 1 | 0.0876 (0.0292) | | |
| Gamma shape parameter | 1 | 9.9908 (3.3114) | | |
| Maximized loglikelihood = -202.49 | | | | |

modified by covariates such as population or treatment (i.e., the regression parameters). Thus, time to first bud increased monotonically with length and starting date of drought. Similarly, plants watered biweekly began budding significantly later than those watered weekly. No population x treatment effects were significant in the watering experiment; such interactions could not be estimated in the drought experiment (see Methods). Time to first bud increased with time to emergence.

A significantly greater proportion of Organ Pipe (49.3%) than Portal (30.0%) plants survived drought treatments to begin flowering ($\chi^2=23.43$, $df=1$, $p<0.001$). As one would expect, the proportion of plants dying without flowering increased with drought length ($\chi^2=210.36$, $df=3$, $p<0.001$). Time of onset of droughts had no effect on the proportion of plants surviving to flower ($\chi^2=1.01$, $df=2$, $p>0.5$). In the watering experiment, there were no significant differences in survival to flowering among populations or experimental treatments (Population, $\chi^2=1.777$, $df=1$, $p=0.183$; Treatment, $\chi^2=0.002$, $df=1$, $p=0.965$).

Organ Pipe plants became established significantly earlier, and completed flowering significantly later, than Portal plants. Treatments had no significant effect on time to last flower. Time to death was not significantly affected by population, treatment, or emergence time.

Size and fecundity

Plants treated with drought or biweekly watering began budding at smaller sizes than those not subjected to drought or given weekly water (fig.3a-b, tables 2.4 - 2.5). Organ Pipe plants began budding at significantly smaller size than Portal plants in all cases (tables 2.4, 2.5). No population x treatment effects were significant.

Families within populations accounted for a significant portion of the variance for height at first bud in the watering experiment (table 2.5). ANOVA conducted separately for each population showed that families accounted for a marginally significant portion of the variance within the Organ Pipe population, and for a nonsignificant portion of the variance within the Portal population. This marginal significance suggests that among-family variation might be largely restricted to the Organ Pipe population (table 2.5); to further examine this issue I conducted unplanned multivariate analysis of variance (MANOVA) on all size traits measured. MANOVA resulted in significant among-family variance for the Organ Pipe but not the Portal population (Wilks' lambda, Organ Pipe families $F=1.595$, $df=116,50.28$, $p=0.032$; Portal families $F=1.09$, $df=136,98.2$, $p=0.334$). Because the data were unbalanced I also examined among-family variance by combining probabilities from univariate ANOVAs for the size traits (Sokal & Rohlf 1981:779). This procedure also suggested significant among-family variance

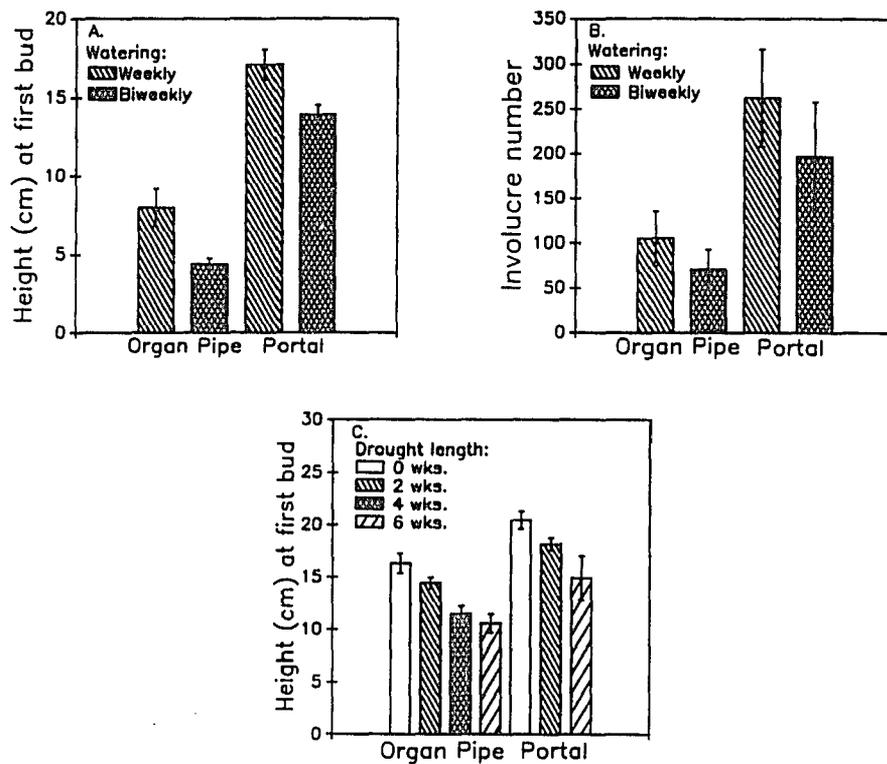


Fig. 2.3. Size consequences of population and experimental treatment (mean \pm s.e.). A) Height at first bud, watering experiment. B) Number of involucre, watering experiment. C) Height at first bud, drought experiment.

Table 2.4. Analyses of variance for height at first bud
for drought experiment.

| Source | df | SS | F | p |
|----------------------|-----|---------|-------|--------|
| AMONG POPULATIONS | | | | |
| Population | 1 | 377.22 | 21.37 | 0.0001 |
| Drought length | 2 | 93.91 | 2.66 | 0.0723 |
| Drought start | 2 | 12.62 | 0.36 | 0.6999 |
| Pop * length | 2 | 80.00 | 2.27 | 0.1062 |
| Pop * start | 2 | 171.90 | 4.87 | 0.0086 |
| Length * start | 4 | 144.57 | 0.40 | 0.0889 |
| Pop * length * start | 2 | 15.61 | 0.44 | 0.6433 |
| Error | 215 | 3795.55 | | |
| ORGAN PIPE | | | | |
| Drought length | 2 | 358.12 | 9.85 | 0.0001 |
| Drought start | 2 | 71.52 | 1.97 | 0.1441 |
| Length * start | 4 | 139.30 | 1.91 | 0.1116 |
| Error | 133 | 2418.94 | | |
| PORTAL | | | | |
| Drought length | 2 | 28.54 | 0.85 | 0.4311 |
| Drought start | 2 | 141.86 | 4.22 | 0.0179 |
| Length * start | 2 | 33.60 | 1.00 | 0.3721 |
| Error | 82 | 1376.60 | | |

Table 2.5. Analyses of variance for watering experiment. F tests and denominator df calculated with Satterthwaite approximation.

| Source | Num df | Denom df | SS | F | p |
|-------------------------------------|--------|----------|--------|-------|--------|
| AMONG POPULATIONS | | | | | |
| HEIGHT AT FIRST FLOWER BUD | | | | | |
| Emergence date | 4 | 59.00 | 59.81 | 8.43 | 0.0001 |
| Experiment | 1 | 24.56 | 22.59 | 12.46 | 0.0017 |
| Population | 1 | 12.14 | 237.77 | 85.61 | 0.0001 |
| Family(Pop) | 63 | 24.64 | 240.81 | 2.11 | 0.0215 |
| Exp * Pop | 1 | 24.48 | 0.52 | 0.29 | 0.5970 |
| Exp * Fam(Pop) | 41 | 59.00 | 74.47 | 1.02 | 0.4597 |
| Error | 59 | 104.60 | | | |
| TOTAL NUMBER OF INVOLUCRES PRODUCED | | | | | |
| Emergence date | 4 | 59.00 | 10.24 | 1.90 | 0.1227 |
| Experiment | 1 | 21.18 | 1.56 | 1.37 | 0.2548 |
| Population | 1 | 0.67 | 8.74 | 20.82 | 0.2226 |
| Family(Pop) | 63 | 20.61 | 74.84 | 1.05 | 0.4656 |
| Exp * Pop | 1 | 21.82 | 0.42 | 0.36 | 0.5525 |
| Exp * Fam(Pop) | 41 | 59.00 | 45.98 | 0.83 | 0.7320 |
| Error | 59 | 79.61 | | | |

Table 2.5, cont'd.

| Source | Num df | Denom df | SS | F | p |
|-------------------------------------|--------|----------|-------|------|--------|
| WITHIN ORGAN PIPE POPULATION | | | | | |
| HEIGHT AT FIRST FLOWER BUD | | | | | |
| Emergence date | 3 | 65.00 | 18.62 | 3.92 | 0.0258 |
| Experiment | 1 | 6.50 | 2.57 | 2.21 | 0.1844 |
| Family | 29 | 5.36 | 98.72 | 3.22 | 0.0883 |
| Exp * Family | 14 | 65.00 | 13.83 | 0.62 | 0.8131 |
| Error | 65 | 28.53 | | | |
| TOTAL NUMBER OF INVOLUCRES PRODUCED | | | | | |
| Emergence date | 3 | 65.00 | 5.47 | 1.44 | 0.2645 |
| Experiment | 1 | 6.41 | 1.12 | 1.22 | 0.3098 |
| Family | 29 | 5.22 | 32.33 | 1.34 | 0.3967 |
| Exp * Family | 14 | 65.00 | 10.76 | 0.61 | 0.8263 |
| Error | 65 | 22.79 | | | |

Table 2.5, cont'd

| Source | Num df | Denom df | SS | F | p |
|-------------------------------------|--------|----------|--------|------|--------|
| WITHIN PORTAL POPULATION | | | | | |
| HEIGHT AT FIRST FLOWER BUD | | | | | |
| Emergence date | 4 | 39.00 | 18.36 | 2.72 | 0.0436 |
| Experiment | 1 | 18.19 | 17.05 | 7.40 | 0.0139 |
| Family | 34 | 20.43 | 128.26 | 1.54 | 0.1512 |
| Exp * Family | 26 | 39.00 | 62.02 | 1.41 | 0.1619 |
| Error | 39 | 65.93 | | | |
| TOTAL NUMBER OF INVOLUCRES PRODUCED | | | | | |
| Emergence date | 4 | 39.00 | 14.19 | 2.44 | 0.0633 |
| Experiment | 1 | 14.51 | 0.34 | 0.26 | 0.6200 |
| Family | 34 | 13.81 | 36.50 | 0.84 | 0.6760 |
| Exp * Family | 26 | 39.00 | 33.67 | 0.89 | 0.6183 |
| Error | 39 | 56.81 | | | |

in the Organ Pipe but not the Portal population (Organ Pipe $\chi^2=18.77$, $df=8$, $p=0.016$; Portal $\chi^2=8.326$, $df=8$, $p=0.402$).

Involucre production was greatest among Portal plants and plants watered weekly (fig. 2.3c). However, variance was so great that none of the ANOVA model terms was significant. Emergence time had a marginally significant effect on involucre number among Portal plants (table 2.5).

Parents and offspring

Substantial genetic variation within the Organ Pipe, but not the Portal population, was also suggested by results of the offspring/parent experiment. Offspring height at first bud was predicted by parental values for Organ Pipe, but not Portal, plants, according to regression analysis (fig. 2.4a). Similarly, Spearman rank correlations between parents and offspring for time to first bud (fig. 2.4b) were marginally significant for Organ Pipe families but not significant for Portal families.

Intraclass correlations

The results presented above suggest a general pattern: significant variation among populations and within the Organ Pipe, but not Portal population. Intraclass correlations (eq. 1) a useful means of summarizing this information and qualitatively comparing populations. Correlations estimated from

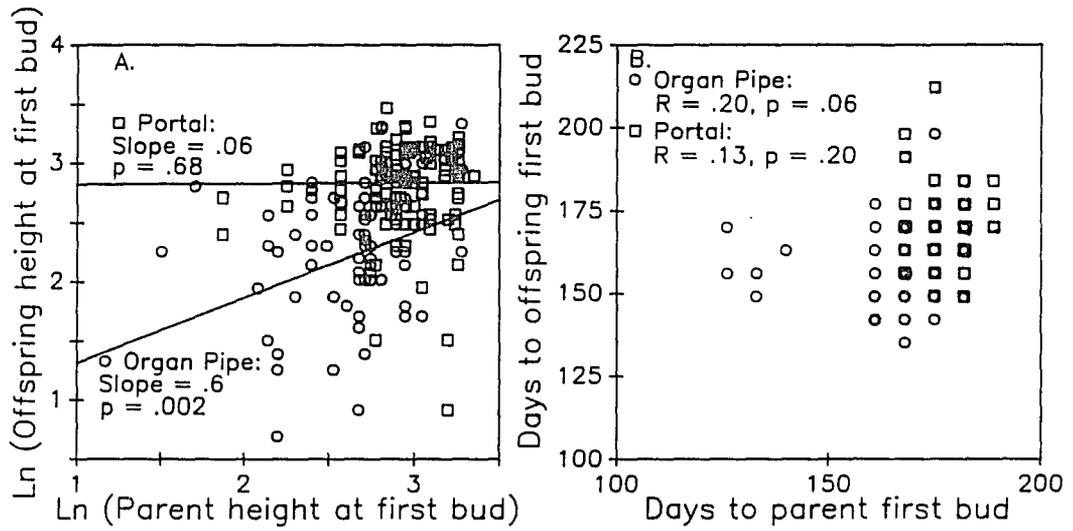


Fig. 2.4. Relationships between parental and offspring values. A) Regression for height at time of first bud. B) Correlation for time to first bud.

both the watering experiment and from the offspring/parent experiment (table 2.6) suggest that there is substantial genetic variance for height at first bud among populations and within the Organ Pipe, but not the Portal population. All correlations for involucre number are small. The estimates derived from the two experiments are roughly comparable. These intraclass correlations, like the regressions in the offspring/parent experiment, could be used to estimate heritabilities if the mating system of these plants were known.

Family means correlations

Populations showed similar patterns of correlation among average trait values within families (table 2.7). As predicted, involucre number was positively and significantly correlated with time to last flower and time to death in each population. The correlation between involucre number and height at first bud was marginally significant for Portal families but nonsignificant for Organ Pipe families. Time to first bud and height at first bud were significantly and positively correlated in both populations. There were positive correlations in both populations between time of first bud and times of last flower and death; these correlations were significant only among Portal families. Several correlations were weaker for the Organ Pipe than for the Portal population, but this difference must be interpreted cautiously because sample sizes differed.

Table 2.6. Intraclass correlation coefficients (variance components estimated with restricted maximum likelihood estimators).

| Trait | Among Populations | Among Families | |
|-----------------------------------|-------------------|----------------|--------|
| | | Organ Pipe | Portal |
| WATERING EXPERIMENT | | | |
| Height at 1st bud | 0.618 | 0.530 | 0.106 |
| Total involucre | 0.117 | 0.110 | 0.000 |
| OFFSPRING FROM DROUGHT EXPERIMENT | | | |
| Height at 1st bud | 0.410 | 0.380 | 0.270 |
| Total involucre | 0.003 | 0.014 | 0.103 |

Table 2.7. Correlations among family means for life history traits (first line is correlation, second line is p correlation $\neq 0$).

| | <u>Time to emergence</u> | <u>Time to 1st bud</u> | <u>Time to last flwr</u> | <u>Time to death</u> | <u>Ht. at 1st bud</u> |
|---------------------------|------------------------------|----------------------------|------------------------------|--------------------------|---------------------------|
| ORGAN PIPE | | | | | |
| Time to 1st bud | 0.2290* | | | | |
| | 0.2236 | | | | |
| Time to last flwr | -0.0408* | 0.1213* | | | |
| | 0.8306 | 0.5230 | | | |
| Time to death | 0.0435* | 0.1853* | 0.9302* | | |
| | 0.8195 | 0.3270 | 0.0001 | | |
| Ht. at time of 1st bud | 0.0828* | 0.8287* | 0.1807* | 0.2038* | |
| | 0.6635 | 0.0001 | 0.3393 | 0.2801 | |
| Total involucres | 0.1176* | -0.1033* | 0.5351* | 0.4454* | 0.0213 |
| | 0.5359 | 0.5869 | 0.0023 | 0.0136 | 0.9109 |

Table 2.7, continued

| | <u>Time to</u> <u>1st bud</u> | <u>Time to</u> <u>last flwr</u> | <u>Time to</u> <u>death</u> | <u>Ht.at</u> <u>1st bud</u> | <u>Total</u> <u>Invol.</u> |
|----------------------|----------------------------------|------------------------------------|--------------------------------|--------------------------------|-------------------------------|
| PORTAL | | | | | |
| Time to emergence | 0.1276* 0.4651 | -0.0111* 0.9495 | 0.0253* 0.8852 | 0.3121* 0.0680 | -0.3188* 0.0620 |
| Time to 1st bud | | 0.3565* 0.0355 | 0.4520* 0.0064 | 0.4192* 0.0122 | 0.0374* 0.8311 |
| Time to last flwr | | | 0.9452* 0.0001 | 0.3157* 0.0647 | 0.3182* 0.0625 |
| Time to death | | | | 0.4532* 0.0063 | 0.4451* 0.0074 |
| Ht. at 1st bud | | | | | 0.2940 0.0864 |

* Correlations involving time variables are Spearman rank correlations; others are Pearson product-moment statistics (see Methods)

Discussion

Variation within and among populations

Flowering time has considerable significance in wild populations of *E. abertianum*. Organ Pipe is drier, hotter, and has more variable rainfall; only about 1-3% of Organ Pipe plants but some 25-65% of Portal plants survive to the summer rainy season (chapter 1). Moreover frosts are rare at Organ Pipe but common at Portal. From an adaptive perspective one might expect Organ Pipe plants to establish and flower earlier, survive droughts better, and flower for a longer period, than Portal plants. Field studies have confirmed two of these predictions for Organ Pipe plants -- earlier onset and later completion of flowering (chapter 1).

The present results strongly suggest that there is a genetic basis for these differences among populations in time and size at onset of reproduction, and time of last flower. Organ Pipe plants were shown to flower significantly earlier and at smaller size than Portal plants in two independent experiments (tables 2.2, 2.4, 2.5). Differences among populations accounted for a large proportion of the variance in size at onset of reproduction (table 2.6). The results of the watering experiment are particularly clear: because there were no differences in the frequency of plants surviving to reproduction among populations or treatments, the results of the failure time analysis cannot be an artifact of differential pre-reproductive mortality. The results also indicate that these

populations differ in the expected direction for two traits not studied in the field: establishment time and drought resistance.

These among-population differences appear to be restricted in scope. Plants from these populations are indistinguishable morphologically. The populations responded similarly to treatments: population x treatment interactions were not significant. Moreover, correlations among the traits measured were generally of the same sign in these populations. As predicted on the basis of the plants' developmental pattern, both populations showed a positive correlation between involucre number and time to last flower and death.

Evidence for local adaptation in size and time at flowering has not been previously reported for desert annuals. Shreve (1951) and Went (1949) noted geographic variation in a few species, but did not consider local adaptation among desert annuals likely, arguing that general adaptations such as germination-inhibiting mechanisms and post-germination plasticity rendered local adaptation unnecessary. Local adaptation in size and time at flowering has been demonstrated in many other plant species, corresponding to latitudinal (Goodwin 1944, Böcher 1949, Reinartz 1984, Lacey 1988) or elevational gradients (Clausen et al. 1940, 1947, 1948, 1951; Clausen & Hiesey 1958), or variation in rainfall periodicity (Burk 1966).

Genetic variation appears to be greater within the Organ Pipe than the Portal population. Parental time and height at first bud appear to be good

predictors of offspring performance in the Organ Pipe, but not the Portal, population (fig. 2.4a-b). In the watering experiment, significant family effects were restricted to the Organ Pipe population (table 2.5). These apparent differences in the genetic structure of these populations cannot be further characterized because the relatedness among the sibs studied was unknown. Present data are insufficient to explain why the peripheral and somewhat isolated Organ Pipe population may include more genetic variation than the relatively central and continuous Portal population.

Drought and flowering in *E. abertianum*

Experimental data (table 2.2) provide strong evidence that onset of reproduction in *E. abertianum* is delayed by drought. Budding was delayed in both populations by isolated drought events as well as by regular but reduced watering. Because seasonal droughts mark the interval between flowering episodes in the field, it is likely that the bimodality in onset of reproductive activity in the field is caused by lack of moisture.

The present results are also consistent with the hypothesis that drought causes the hiatus in flowering within spring-flowering individuals. These experiments did not directly test this prediction, however: in pilot studies it was difficult to simulate droughts severe enough to halt flowering, without also killing the plants. This may be because soils under natural conditions dry much more

slowly than do soils in individual pots. Because at least 35% and as many as 99% of plants die during this hiatus in wild populations (chapter 1), a direct test of this prediction would require prohibitively large garden experiments. Such experiments, moreover, would not permit an examination of among-family variation because of the small number of seeds produced by most wild-grown plants. Despite this lack of direct evidence, drought seems a likely explanation for the within-individual flowering hiatus, because a) these hiatus occur in wild plants only during periods of drought; b) moisture limitation has been shown above to delay onset of budding; and c) flower production is anatomically dependent on growth, and therefore on moisture availability.

Physiological studies show that flowering involves numerous factors (e.g., temperature, photoperiod, nutrient concentrations, rates of physiological processes) which may interact unpredictably (Bernier 1986). The present results thus address only a narrow issue -- the effect of moisture limitation on flowering in *E. abertianum* -- and not the broader question of how flowering is controlled in general. The latter has not been fully answered for any plant species.

Comparative evidence on drought and flowering

Is this response to drought by *E. abertianum* unusual for an annual plant? Drought-induced flowering is often thought to be the rule among annuals, especially those from deserts (e.g., Leopold & Kriedemann 1975, Turner & Begg

1978, Rathcke & Lacey 1985). However, this contention is not supported by the present study, nor by the only previous study of this problem in desert annuals. Mott and McComb (1975) showed that flowering was delayed by drought in two Australian winter-flowering annual composites, *Helipterum craspedioides* and *Helichrysum cassinianum*, but the summer-flowering grass *Aristida contorta* flowered earliest under intermediate watering treatments.

There is little evidence that drought induces flowering in any herbaceous annual. Drought inhibition of flowering has been documented in barley (Nicholls & May 1963, Husain & Aspinall 1970), sunflower (Marc & Palmer 1976), sorghum (Whiteman & Wilson 1965), jute (Johansen et al. 1985), nettle (Boot et al. 1986), *Lolium temulentum*, *Pharbitis nil*, and *Xanthium strumarium* (Aspinall & Husain 1970), and in *Teesdalia nudicaulis* (Newman 1965). In pearl millet, drought delays flowering but causes an increased proportion of tillers to flower (Mahalakshmi & Bidinger 1985a, 1985b; Bidinger et al. 1987). On the other hand, wheat appears to flower earliest under intermediate watering treatments (Angus & Mancur 1977).

Because water status is closely related to temperature and nutrient status, these experiments cannot be interpreted in terms of the independent physiological effect of water status. In the present context, the important issue is ecological: does drying of soil tend to induce flowering in annual plants? The results surveyed above suggest that the opposite may more often be true.

Would drought-induced flowering necessarily be adaptive if it did exist in a desert annual? Seed number and seed size are reduced by water stress during flowering and fruiting in virtually every plant species studied (Salter & Goode 1967, Slatyer 1973, Fischer 1973, Fischer & Turner 1978). Carbohydrate sources are severely limited during drought, because drought inhibits both new assimilation (Gates 1968, Yoshida 1972, Slatyer 1973) and translocation of carbohydrates (Wardlaw 1968). Translocation of nutrients is reduced, proteolysis increased, and protein synthesis inhibited during drought (Crafts 1968, Gates 1968, Wardlaw 1968). Moreover, drought inhibits microsporogenesis, pollen grain germination, and fertilization (Slatyer 1973, Fischer & Turner 1978).

These sequelae to water stress do not by themselves render drought-induced flowering impossible for an herbaceous annual, but they do restrict the circumstances in which the benefits of such a mechanism might actually outweigh its costs. There is an additional reason why drought-induced flowering could be expected to be rare in herbaceous annuals: the developmental dependence of current reproduction on current growth is not peculiar to eriogonums, but is a rather widespread pattern among herbaceous annuals.

Drought hastens completion of the life cycle in annuals by causing rosette and leaf senescence, and sometimes by speeding the maturation of previously set fruit (Newman 1965, Gates 1968). Such early maturation of fruit could potentially result in a net fitness gain for a plant dying of water stress. However,

this mechanism is very different from the drought-induced flowering often claimed for desert annuals. There have been no studies on the fitness consequences of accelerated maturation of fruit as a response to drought.

Implications for desert annual life histories

If drought does inhibit, rather than induce, flowering in many desert annual species, several patterns can be predicted: 1) death prior to seed set should be common, even among plants large enough to potentially reproduce; 2) because drought limits resource availability, flowers produced at the end of the season should often be unable to mature fruit; 3) if they are severe enough, mid-season droughts should lead to multiple flowering episodes even among short-lived annuals; 4) because temperatures are frequently not high enough to permit flowering during the winter, such multiple flowering episodes should be more common among summer-flowering species; 5) plants which are normally "ephemeral" should sometimes survive to a second rainy season when provided extra moisture; and 6) multiseason life histories should be fairly common in areas with both winter and summer rains.

These predictions differ substantially from the traditional view of desert annual life histories. The latter view -- based on temperature-dependent germination and drought-induced flowering -- includes the claims that desert annuals 1) usually germinate only in response to rainfall heavy enough to

guarantee successful seedset; 2) flower in response to drought; 3) consequently are almost always able to set some seed (e.g., Went 1948, 1949, 1955; Went & Westergaard 1949; Lacey 1986); and 4) are almost all "ephemeral," i.e., their activity is restricted to a single growing season, and their life cycles are often completed in 6-8 weeks (Shreve 1951).

Do desert annuals "almost always" set some seed before dying? Published evidence supporting this hypothesis is casual, and generally does not distinguish between seed set by species and seed set by individuals (Went 1948,1949,1957; Went & Westergaard 1949; Juhren et al. 1956). All other studies have reported a different result: survivorship to maturity varies considerably, but in most years a large fraction (often a majority) of individuals die without setting seed (Shreve 1951; Tevis 1958a, 1958b; Klickoff 1966; Beatley 1967; Loria & Noy-Meir 1979-80; Inouye 1980; Burk 1982; chapter 1; D.L. Venable, unpublished data).

There are scanty data bearing on several of the other predictions based on inhibition of flowering by drought. In Delph's (1986) demonstration of moisture limitation of fruit and seed set in the Sonoran Desert annual *Lesquerella gordonii*, flowers produced at the end of the season failed to set fruit. Shreve (1951) stated that multiple episodes of flowering corresponding with rainfall are common within individual Sonoran Desert winter annuals; such phenologies have also been reported in two summer-germinating *Bouteloua* species in California (Went 1948) and a winter-germinating *Eriastrum* in Arizona

(T. Philippi, pers. comm.). Shreve (1951) also noted that survivorship into a second rainy season or even a second year is common among normally "ephemeral" plants found growing near irrigation ditches and roadsides.

Reports are common of plants found "out of season" (e.g., Went 1948a, Mott and McComb 1975), suggesting that multiseason life histories may not be simply an oddity of a few taxa. Almost all annual eriogonums have two flowering seasons (Reveal 1968). Multiple flowering seasons have been reported from Australia, California, and New Mexico in *Ambrosia*, *Aristida*, *Chenopodium*, *Cordylanthus*, *Lessingia*, *Linum*, and *Palafoxia* species (Mott 1973, Zabriskie 1979, Kemp 1983). Among native Arizona annuals multiseason phenologies are commonly seen in *Argemone*, *Atriplex*, *Cirsium*, *Erigeron*, *Heterotheca* (pers. obs.), and *Machaeranthera* (R. Holmes, unpublished) species. Optimization models of annual plant life histories (chapter 1; chapter 4) suggest that multiseason life histories can be favored by selection even when survival to a second season is an uncommon event.

This brief list suggests that the full array of desert plant life histories may be considerably richer than is usually appreciated. For example, there are a number of taxa which include weakly perennial as well as multiseason annual variants, including *Allionia*, *Baileya*, and *Erioneuron* species (pers. obs.; T.R. Van Devender, pers. comm.). There are also species, such as *Bouteloua barbata*, which are summer annuals in Arizona but winter annuals at the southern desert

margin near Guaymas, Sonora (Shreve 1951; T.R. Van Devender, pers. comm.), and species with two generations within a year (e.g., *Galium proliferum*, *Aristida adscensionis*, *Parietaria* sp. (Van Devender et al., in press; T.R. Van Devender, pers. comm.)). This diversity of life histories should not remain so poorly studied.

Adaptative and non-adaptive explanations for variation

Results presented here provide support for the hypothesis of local adaptation of flowering time in *E. abertianum*. The among-population differences have considerable demographic significance in wild populations (chapter 1), are consistent with trends among several additional populations (table 2.1), and appear to have a genetic basis (tables 2.2, 2.4, 2.5; fig. 2.4a-b). Because there is also biogeographic evidence suggesting a Chihuahuan desert origin for *E. abertianum*, and fossil evidence demonstrating that the species invaded the Sonoran Desert during a cooler and wetter period than the present (chapter 1), the case for adaptation is fairly strong.

Much of the variation within populations appears to be a consequence of a major environmental factor -- drought. Results reported here demonstrate that drought delays onset of flowering. Because severe droughts separate flowering seasons in wild populations, and because among-family variance for reproductive traits appears significant only in the Organ Pipe population, it seems difficult to

avoid the conclusion that drought is probably a major cause of the bimodal distribution of flowering times in wild populations. As noted above, drought also appears likely to cause the within-individual hiatus in flowering, although evidence for this is somewhat weaker. Field studies (chapter 1) indicate that spring-flowering plants consistently have greater survivorship and fecundity than non-spring-flowering plants, posing a difficulty for adaptive explanations.

Life histories, particularly those of plants, have been generally viewed for at least 20 years (Cody 1966, Williams 1966) as consequences of tradeoffs between growth, survival, and reproduction; the latter are viewed as independent compartments competing for limited resources. The present paper and related field studies lend support to the suggestion (Watson & Casper 1984) that it may be useful to refine this view. Growth and reproduction in *E. abertianum* are tightly coupled by an invariant anatomy, and it appears that this coupling itself leads to some of the most conspicuous aspects of the life history of this species.

While drought appears to be a major factor in the life history of this species, it is interesting to note that multiple flowering episodes within individuals have also been predicted as adaptive strategies. In an optimization model by King and Roughgarden (1982), multiple flowering episodes were shown to maximize total seedset of an annual plant if the latter experiences sufficiently large changes in growing conditions. However, *E. abertianum* appears to violate the assumptions of this model. Flowering activity in this species is strongly

affected by the environment, but King and Roughgarden (1982; see also Vincent & Pulliam 1980, Schaffer et al. 1982, Chiariello & Roughgarden 1984) assumed that flowering activity is freely determined by the plant. To make matters worse, this environmental response appears to be fairly general among herbaceous annuals. Moreover, demographic evidence suggests that annual seedset at Organ Pipe might be increased by a 100% switch to spring flowering, but the multiseason habit appears to be invariant in this species and its annual congeners (Reveal 1968, chapter 1).

While the similarity between model and observations thus seems coincidental in this case, it is instructive to note the essential role of comparative evidence in reaching this conclusion. Unfortunately there is no guarantee that comparative evidence will always be so clear, suggesting that it may not always be possible to examine the relative merits of adaptive and non-adaptive explanations for our observations.

CHAPTER THREE

Perennation and the Persistence of
Annual Life Histories

Life histories are often described as distinct syndromes, e.g., perennial vs. annual or biennial habits. However, such syndromes are widely recognized to be approximations at best. For example, it is well known that annual plants sometimes live for more than one year (e.g., Beatley 1970, Sano 1980), biennials frequently live for more than two (Werner & Caswell 1977), and many perennial herbs begin flowering in their first year but only occasionally survive into additional years.

In the face of such variation, it seems useful to ask whether traits characterizing such life history syndromes vary discretely or continuously. If the variation is continuous, can we expect such syndromes to persist, or are they likely to grade into one another? In this chapter I consider empirical evidence on the discreteness of life history syndromes in one population of annual plants. The results suggest that the chance of surviving into a second year (hereafter "perennating") may have some genetic basis, but the variation appears to be continuous. Using a simple model of size-dependent demography and Lande's (1982) quantitative genetic model of life history evolution, I then examine selection on this ability to perennate.

Eriogonum abertianum Torr. (Polygonaceae) is an annual plant of the Sonoran and Chihuahuan Deserts. In some years perennation occurs in about

0.5% or fewer of individuals of *E. abertianum* at Organ Pipe Cactus National Monument, Arizona; in other years perennation does not occur (chapter 1). Occasional perennation has been reported in many other species of annual plants (Beatley 1970, Gagnon et al. 1980, Sano et al. 1980, Oka & Sano 1981, Boyce & Cunningham 1982, Waite & Hutchings 1982, Oka 1983, Waite 1984, Morishima 1985, Keddy 1987). Such perennation has often been assumed to be adaptive, but there are no studies concerning its fitness consequences.

MATERIALS AND METHODS

Seeds were collected in February 1986 from a study population located on a south-facing slope of the Ajo Mts. at Organ Pipe Cactus National Monument; the site is described in chapter 1. Families of seeds collected from maternal plants which had perennated were compared with families from maternal plants in their first season. Perennation by maternal plants was determined on morphological grounds: perennating maternal plants were all >10 cm in height, lacked rosette leaves, and had well-branched inflorescences and fibrous stems, while the comparison group were <5 cm rosettes without fibrous stems or extensive branching.

This experiment therefore compared plants which had perennated with a random sample of the population -- not with plants which had not perennated.

Such a conservative test was necessary because there is no way to distinguish perennating from non-perennating plants prior to the death of the latter -- by which time their seeds are no longer available.

In March 1986 seeds were planted in the greenhouse in pots filled with clean sand, covered with vermiculite, and misted daily until cotyledons emerged. Seedlings were thinned to one per pot upon emergence, by removing all but the seedling closest to the center of the pot. Four pots were planted for each maternal plant; 25 families of each type were used. Plants were positioned randomly in the greenhouse. Plants experienced natural photoperiod and weekly watering to field capacity. An evaporative cooler operated from mid-May to mid-September. Greenhouse conditions were thus benign relative to natural conditions. In many respects, however, these plants perform similarly in the greenhouse and field (chapter 2).

Height to highest node was recorded at time of first bud and at anthesis. Involucre number was counted at cessation of flowering. Dates of emergence, first flower bud, anthesis, last flower, and death, were recorded for all plants.

Statistical analysis

All variables defined as "time until an event occurs" were analyzed using accelerated failure time models (Lee 1980, Lawless 1982) to compare parental types. These models are appropriate for event time data because one can

include data which are "right-censored," (e.g., plants which die before a response occurs), because normality of data need not be assumed, and because covariates can be included in the model with fewer assumptions than for linear models (chapter 2). In the present case, all event time data were assumed to have an underlying gamma distribution. Because analysis of emergence date showed no significant effect of parental type (table 3.2), emergence date was used as a covariate in all subsequent analyses.

All other variables were analyzed with analyses of variance (ANOVA) after being transformed to assure normality. Families were nested within parental type, and emergence date was treated as a block effect. Because data were unbalanced, all models were analyzed using SAS Type III sums of squares (Freund et al. 1986) and approximate F tests (Milliken & Johnson 1984).

The relationships between time to last flower, time to death, and fecundity, were examined with rank correlation analysis. To test for differences between parental types in the relationship between date of last flower and involucre number, I analyzed a heterogeneity of slopes model.

RESULTS

ANOVA revealed no significant differences among parental types for height at onset of reproduction or for involucre number (table 3.1). However, significant differences were revealed among families within parental types for both height characters.

Failure time analyses (table 3.2) resulted in a somewhat different picture. No significant effects of parental type were revealed for time to first flower bud or anthesis, but time to last flower and time to death both showed marginally significant effects of parental type ($p=.06$ and $p=.09$, respectively).

No other trait varied significantly among groups (table 3.1). Neither among- nor within-group variance for involucre number was significant.

As expected (chapter 2) involucre number increased significantly with time to last flower and death (table 3.3). Fecundity appeared to increase with longevity at the same rate for the two parental types, because the term for parental type x last flower in the heterogeneity of slopes model was not significant ($F=0.99$, $df=1$, $p=0.3315$).

DISCUSSION

The failure time analyses (table 3.2) for time to last flower and death suggest that there may be some genetic variance for these traits. While the

Table 3.1. Effect of parental type on size and fecundity traits: analyses of variance.

| Source | Num df | Denom df | SS | F | <i>p</i> |
|-----------------------------------|--------|----------|-------|------|----------|
| HEIGHT AT FIRST FLOWER BUD | | | | | |
| Emergence date | 3 | 19.00 | 4.63 | 4.58 | 0.01 |
| Parent type | 1 | 17.74 | 0.62 | 0.94 | 0.34 |
| Family (Type) | 28 | 19.00 | 19.99 | 2.12 | 0.04 |
| Error | 19 | 6.40 | | | |
| HEIGHT AT ANTHESIS | | | | | |
| Emergence date | 3 | 19.00 | 0.95 | 3.66 | 0.31 |
| Parent type | 1 | 19.13 | 0.06 | 0.28 | 0.60 |
| Family (Type) | 28 | 19.00 | 6.94 | 2.86 | 0.01 |
| Error | 19 | 1.65 | | | |
| NUMBER OF INVOLUCRES | | | | | |
| Emergence date | 3 | 19.00 | 9.51 | 1.67 | 0.21 |
| Parent type | 1 | 13.25 | 3.67 | 0.28 | 0.22 |
| Family (Type) | 28 | 19.00 | 64.59 | 1.22 | 0.33 |
| Error | 19 | 36.04 | | | |

Table 3.2. Effect of parental type on time until life history event:

failure time analyses.

| <u>Variable</u> | <u>df</u> | <u>Regression Parameter (s.e.)</u> | <u>χ^2</u> | <u><i>p</i></u> |
|---------------------------------|-----------|--|----------------------------|-----------------|
| TIME TO EMERGENCE | | | | |
| Intercept | 1 | 4.70 (.002) | 5135247.00 | 0.0001 |
| Parental type | 1 | | 0.01 | 0.9055 |
| General population | 1 | 0.00 (0.002) | 0.01 | 0.9055 |
| Survive > 1 yr | 0 | 0 | 0 | 0 |
| Gamma scale parameter | 1 | 0.01 (.004) | | |
| Gamma shape parameter | 1 | 10.00 (4.70) | | |
| Maximized loglikelihood = 71.95 | | | | |
| TIME TO FIRST FLOWER BUD | | | | |
| Intercept | 1 | 3.93 (.06) | 3883.17 | 0.0001 |
| Emergence date | 1 | 0.009 (.002) | 15.02 | 0.0001 |
| Parental type | 1 | | 0.58 | 0.4775 |
| General population | 1 | 0.028 (.037) | 0.58 | 0.4775 |
| Survive > 1 yr | 0 | 0 | 0 | 0 |
| Gamma scale parameter | 1 | 0.126 (.018) | | |
| Gamma shape parameter | 1 | -0.817 (.447) | | |
| Maximized loglikelihood = 28.10 | | | | |

Table 3.2, cont'd.

| <u>Variable</u> | <u>df</u> | <u>Regression Parameter (s.e.)</u> | <u>χ^2</u> | <u><i>p</i></u> |
|-------------------------|-----------|--|----------------------------|-----------------|
| TIME TO ANTHESIS | | | | |
| Intercept | 1 | 4.170 (.037) | 13050.50 | 0.0001 |
| Emergence date | 1 | 0.005 (.002) | 11.67 | 0.0006 |
| Parental type | 1 | | 0.46 | 0.4965 |
| General population | 1 | 0.017 (.024) | 0.46 | 0.4965 |
| Survive > 1 yr | 0 | 0 | 0 | 0 |
| Gamma scale parameter | 1 | 0.084 (.011) | | |
| Gamma shape parameter | 1 | -0.919 (.366) | | |

Maximized loglikelihood = 47.38

TIME TO LAST FLOWER

| | | | | |
|-----------------------|---|---------------|---------|--------|
| Intercept | 1 | 5.189 (.087) | 3595.16 | 0.0001 |
| Emergence date | 1 | 0.006 (.004) | 1.92 | 0.1656 |
| Parental type | 1 | | 3.43 | 0.0642 |
| General population | 1 | -0.118 (.064) | 3.43 | 0.0642 |
| Survive > 1 yr | 0 | 0 | 0 | 0 |
| Gamma scale parameter | 1 | 0.224 (.022) | | |
| Gamma shape parameter | 1 | -0.019 (.407) | | |

Maximized loglikelihood = 4.00

Table 3.2, cont'd.

| <u>Variable</u> | Regression | | | |
|--------------------------------|------------|-------------------------|----------------------------|-----------------|
| | <u>df</u> | <u>Parameter (s.e.)</u> | <u>χ^2</u> | <u><i>p</i></u> |
| TIME TO DEATH | | | | |
| Intercept | 1 | 5.364 (.094) | 3240.97 | 0.0001 |
| Emergence date | 1 | 0.004 (.004) | 1.48 | 0.2234 |
| Parental type | 1 | | 2.93 | 0.0869 |
| General population | 1 | -0.101 (.059) | 2.93 | 0.0869 |
| Survive > 1 yr | 0 | | 0 | 0 |
| Gamma scale parameter | 1 | 0.208 (.028) | | |
| Gamma shape parameter | 1 | 0.612 (.505) | | |
| Maximized loglikelihood = 4.77 | | | | |

Table 3.3. Correlations between time to last flower, time to death, and involucre number. First line = Spearman correlation coefficient R, second line = significance of $H_0: R=0$.

NON-PERENNATORS

| | <i>Last Flwr</i> | <i>Death</i> | <i>Total Involucres</i> |
|---------------|----------------------|--------------|-----------------------------|
| <i>Last</i> | 1 | | |
| <i>Flwr</i> | 0 | | |
| <i>Death</i> | .94 .0001 | 1 0 | |
| <i>Total</i> | .54 | .46 | 1 |
| <i>Invol.</i> | .0017 | .0094 | 0 |

PERENNATORS

| | <i>Last Flwr</i> | <i>Death</i> | <i>Total Involucres</i> |
|---------------|----------------------|--------------|-----------------------------|
| <i>Last</i> | 1 | | |
| <i>Flwr</i> | 0 | | |
| <i>Death</i> | .93 .0001 | 1 0 | |
| <i>Total</i> | .61 | .49 | 1 |
| <i>Invol.</i> | .0034 | .0034 | 0 |

results were marginally significant statistically, the inherently conservative nature of this experiment suggests that the differences are likely to be real. Such differences appear to be restricted to traits related to the end of the life cycle.

The frequency distributions for time to death (fig. 3.1) indicate that offspring of the two parental types vary continuously, with considerable overlap; distributions for time to last flower show the same general pattern. It seems reasonable to suggest that perennating plants may simply represent the right-hand tail of a continuous longevity distribution. Present data are inadequate to evaluate this hypothesis, but it is consistent with the failure time analyses because one would expect significant among-group differences when comparing the right-hand tail of the distribution with a random sample of the entire distribution. A basic qualitative similarity between the two groups is also suggested by the heterogeneity of slopes model, which revealed no differences between groups in the rate at which fecundity increases with longevity.

Persistence of the annual habit

These results raise an interesting question: under what circumstances is the annual habit likely to persist in the presence of genetic variation for perennation? This question is equivalent to asking whether survivorship of adults is likely to increase when small, given appropriate genetic variation. The quantitative genetic framework suggested by Lande (1982) is an appropriate one

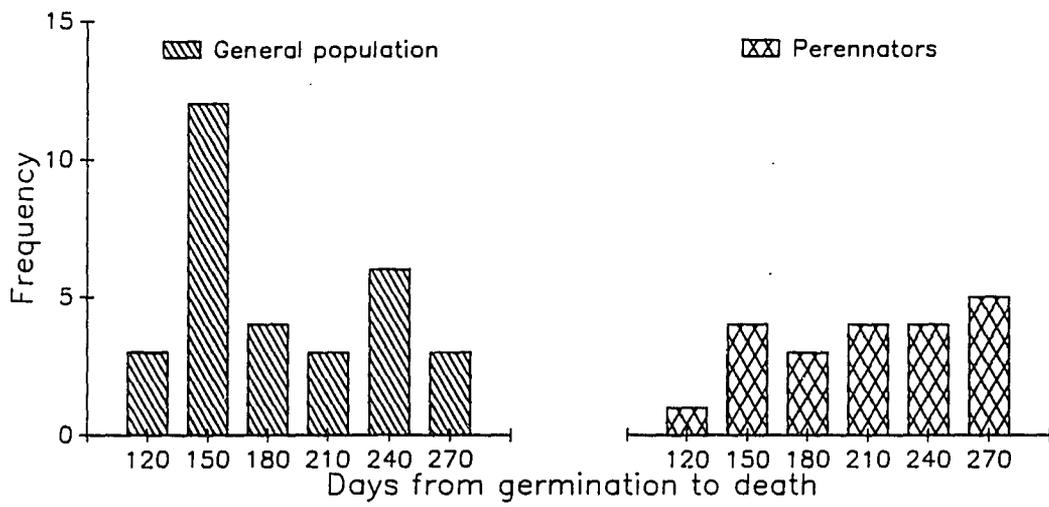


Fig. 3.1. Frequency distribution for time between germination and death, for general population and for perennators.

for this problem. In Lande's model the change in the mean value of a trait in each generation is given by

$$\Delta \mathbf{z} = \mathbf{G} \mathbf{s} , \quad (1)$$

where \mathbf{z} is a vector of trait means, \mathbf{G} is a genetic variance/covariance matrix, and \mathbf{s} is the "selection gradient" defined by

$$s_i = \partial r / \partial z_i, \quad (2)$$

where r is the intrinsic rate of increase of the population. For a single trait the model reduces to

$$\Delta z = \text{Var}(z) \partial r / \partial z, \quad (3)$$

For a population without age structure

$$r = \ln (P_a + c B P_0) \quad (4)$$

where P_a is the survivorship probability of adults, P_0 is a newborn's probability of reaching maturity, B is the mean fecundity of adults, and c is the relatedness of parents to their offspring (Charnov & Schaffer 1973). The assumption of a lack of age structure is appropriate for populations which are principally annual with very small P_a .

Following Lande's (1982) suggestion that simple growth models might provide a useful basis for examining life history evolution, I use a model of size-dependent demography to derive expressions for eq.(4). The alternative of beginning with a transition matrix model is inappropriate because survivorship

probabilities are non-negative, and near zero breeding values must be distributed non-normally -- violating the assumptions of eq.(1). The size-dependent model which I use is a simplification of the models developed by Stearns and Koella (1986).

Assume that the juvenile mortality rate $\mu_j(t)$ is related to size $S(t)$ by some function such as

$$\mu_j(t) = a_0/\gamma S(t) , \quad (5)$$

and that the adult mortality rate $\mu_a(t)$ is related to size at maturity $S(\alpha)$ by some function such as

$$\mu_a(t) = a_0/\phi S(\alpha) . \quad (6)$$

Here a_0 is an environmental component of mortality, and the constants γ and ϕ describe the extent to which size reduces mortality. The results discussed below do not change qualitatively if the size terms in (5) and (6) are raised to a constant power. Next assume that fecundity is an increasing function of size at maturity such as

$$B = F [S(\alpha)]^\tau , \quad (7)$$

where F and τ are constants. Finally, assume that size at each time t is given by the von Bertalanffy equation

$$S(t) = A (1 - B e^{-kt}) , \quad (8)$$

where A is the limiting size of the organism, k is the growth rate, and B is the difference between limiting size and size at birth, given as a proportion of the limiting size.

Expressions for P_0 and P_a -- finite probabilities of surviving a time interval -- can be found by substituting (5) and (6) respectively, subject to (8) into

$$\frac{dP}{dt} = -P(t) \mu(t) , \quad (9)$$

and integrating from 0 to α for P_0 and from 0 to π , the season length, for P_a .

Doing so and simplifying yields

$$P_0 = \exp \left[\frac{a_0}{A k \gamma} \ln \left(\frac{1 - B}{e^{a_0 k} - B} \right) \right] \quad (10)$$

and

$$P_a = \exp \left(- \frac{\pi a_0 e^{k\alpha}}{A \beta (e^{k\alpha} - B)} \right) . \quad (11)$$

Note that a formulation like (11) allows us to consider cases where the probability of surviving to a second year is finite but very small.

Substituting (7, 10, 11) into (4) finally gives

$$\lambda = \exp \left(- \frac{\pi a_0 e^{k\alpha}}{A \beta (e^{k\alpha} - B)} \right) + \{c F [S(\alpha)]^r\} \exp \left[\frac{a_0}{A k \gamma} \ln \left(\frac{1 - B}{e^{a_0 k} - B} \right) \right], \quad (12)$$

with $r = \ln(\lambda)$. Although this model includes a number of parameters which could be subject to natural selection, I restrict my attention to those affecting perennation.

Analysis: age at maturity

Consider the evolution of age at maturity α . Equation (12) implies a trade-off between juvenile survivorship on the one hand, and adult survivorship and fecundity on the other. Differentiating r with respect to α , and simplifying, yields

$$\frac{\partial r}{\partial \alpha} = \frac{-P_a \ln(P_a) B + cBP_0 \{B\tau - e^{k\alpha} [\ln(P_0) / \ln((1-B)/(e^{k\alpha} - B))]\}}{\lambda (e^{k\alpha} - B)} \quad (13)$$

This derivative is usually negative for P_a near 0 or 1, but may be positive for intermediate values. To see this, note first that the sign of (13) depends on the numerator only. The left-hand term -- $-P_a \ln(P_a) B$ -- is never negative; $P_a \ln(P_a)$ is zero at $P_a = 1$, approaches zero asymptotically as P_a approaches zero, and has an intermediate maximum at $P_a = e^{-1}$ ($\approx .37$). On the other hand, the right-hand term in the numerator of (13) is negative for most realistic parameter values. To check this assertion, notice that $[\ln(P_0) / \ln((1-B)/(e^{k\alpha} - B))]$ is always positive, because the arguments of both logarithms are < 1 , and this positive ratio is multiplied by an exponential term. Unless $B\tau$ is very large, then, the

right-hand term in the numerator of (13) is negative. At very low or very high values of P_a , the direction of selection will thus be for reduced age at maturity.

Analysis: limiting size

The probability of perennating in (11) is also affected by the limiting size A . To consider selection on this trait, differentiate (12) and simplify, to get

$$\frac{\partial r}{\partial A} = \frac{-P_a \ln(P_a) + cBP_0 \{\tau + \ln(P_0)\}}{A\lambda} \quad (14)$$

Analysis of (14) is closely analogous to that for (13). The sign of (14) again depends on the numerator. The left-hand term in the numerator is again near zero for very large or small values of P_a , and the right-hand term is negative if $\tau + \ln(P_0) < 0$. Because biological realism demands $\tau < 1$ the right-hand term is always negative if $P_0 < e^{-1}$ ($\approx .37$). At very high or very low adult survivorship probabilities, then, selection favors a reduction in the limiting size, unless juvenile survivorship probabilities are high. Note that juvenile survivorship probabilities less than .37 are not unusual among populations of annual plants (chapter 1, 2).

Correlated characters

Finally, consider the simultaneous evolution of P_a when both A and α are subject to selection, using (1). The total change in P_a in each generation is given by

$$\Delta P_a = \frac{\partial P_a}{\partial \alpha} \Delta \alpha + \frac{\partial P_a}{\partial A} \Delta A . \quad (15)$$

Expanding (15) and factoring out terms which do not affect the sign of ΔP_a yields

$$\begin{aligned} \text{sgn}(\Delta P_a) = \text{sgn} & \left[\frac{B}{(e^{k\alpha} - B)} \text{var}_g(\alpha) \left(\frac{\partial r}{\partial \alpha} + \text{cov}_g(\alpha, A) \frac{\partial r}{\partial A} \right) \right. \\ & \left. + \frac{1}{A} \left(\text{cov}_g(\alpha, A) \frac{\partial r}{\partial \alpha} + \text{var}_g(A) \frac{\partial r}{\partial A} \right) \right], \quad (16) \end{aligned}$$

where sgn , the signum function, gives the sign of its argument. If the signs of the two partial derivatives are the same, the covariance can affect the rate, but not the direction, of change. This is a consequence of the so-called Schwarz inequality, which imposes boundaries on the magnitude of a covariance as compared with the related variances. As shown above, the signs of both partial derivatives are likely to be negative for very small or large values of P_a , especially if $P_0 < .37$. If the signs of the partial derivatives are different, however, the direction of evolution cannot be determined without knowing values for all of the terms in (16).

Conclusions

These theoretical results demonstrate that the annual habit can persist over a wide range of circumstances in the presence of genetic variation for perennation. The range of conditions under which the annual habit can persist may be even greater than the present analysis indicates, because these results were derived without assumptions about trade-offs between fecundity and adult survivorship. Thus life histories may tend to cluster into more or less discrete syndromes even when the relevant traits vary continuously.

The results also show that selection can favor reduction in the age at maturity and limiting size when adult survivorship probabilities are very high. However, it is not clear how often adult survivorship probabilities are high in non-age-structured populations.

CHAPTER FOUR

Models of Optimal Carbon Allocation Schedules in
Annual Plants: Practical DifficultiesI. Introduction

Many recent studies of life history evolution have addressed the dynamics of resource allocation throughout the lives of organisms, many using the techniques of optimal control theory and dynamic programming (e.g., Cohen 1971; Paltridge & Denholm 1974; León 1976; Macevicz & Oster 1978; Mirmirani & Oster 1978; Vincent & Pulliam 1980; Goodman 1982; King & Roughgarden 1982a, 1982b; Schaffer et al. 1982; Chiariello & Roughgarden 1984; Iwasa & Roughgarden 1984; Hom 1987, 1988; Kozłowski & Ziólko 1988). This approach represents a conceptual advance over traditional studies of "reproductive effort" (i.e., the fraction of resources devoted to reproduction) for several reasons. Most importantly, a given measurement of reproductive effort does not uniquely define the organisms' life history: one could find organisms which at the time of measurement have allocated identical percentages of standing carbon or some other resource, but which have quite different histories of resource allocation (Schaffer 1983). In contrast, successful models of the time course of resource allocation could allow one to uniquely predict the organisms' status at every moment. Moreover dynamic models of resource allocation can, in principle,

capture a good deal of the physiological and developmental processes underlying life history evolution.

Progress in the development of this theoretical approach has been slow, however. The difficulty of the mathematics has tended to restrict the models to extremely simple cases. For example, although an annual plants' expectation of survival seems likely to affect its optimal resource allocation schedule, previous studies have assumed 100% survivorship to the end of the growing season. Similarly, most previous studies have treated the organisms -- in most cases, annual plants -- as bodiless entities without constraints on the manner in which resources may be allocated. It seems reasonable to suggest that underlying biological factors -- e.g., developmental, anatomic, and physiological mechanisms -- must impose such constraints.

In this chapter I suggest ways in which models of carbon allocation of annual plants can be made more biologically realistic. First I examine the effects of mortality on optimal schedules of carbon allocation in annual plants. I show that mortality affects the timing of the onset of reproduction -- contrary to the conclusion reached in the static model of Kozłowski and Wiegert (1986) -- and can even change the qualitative nature of the optimal solutions. I also demonstrate a simple method by which allometric growth constraints can be

incorporated in models of herbaceous plant growth, and discuss the limits of the phenomenological method used.

If the rate of theoretical progress in dynamical models of resource allocation has been sluggish, it has nevertheless exceeded that of empirical tests of these models. There have been several attempts at quantitative tests (King & Roughgarden 1983, Chiariello & Roughgarden 1984, Hom 1988). These have had mixed results, frequently seeming to capture some important qualities of the observed life histories but often erring in quantitative predictions.

It therefore seems useful to examine a second issue: the potential of control-theoretic models to guide empirical research. In the numerical analyses below I do so by investigating the sensitivity of these models to departures from optima, as well as their sensitivity to variation in model parameters. These analyses assume that optimization models can in principle describe the outcome of evolutionary processes. While there are reasons to doubt that this is necessarily so (Gould & Lewontin 1979), the questions examined below concern problems involved in applying this assumption.

In some cases studied below, the parameters which are varied correspond to the kind of random variation encountered by individual plants, e.g., microhabitat-level variation in growth conditions. It is a well-known result in control theory that when such parameters vary randomly, optimal controls need

to be formulated as "closed loop" or feedback controls, in which the optimal strategy depends on the state of the system (Bryson & Ho 1975, Cruz 1972). Biologically this is analogous to the idea of adaptive phenotypic plasticity in the face of a variable environment. The third issue considered in this chapter is the extent to which closed loop control models are likely to be useful in the study of phenotypic plasticity.

II. Carbon allocation and mortality

A model

Consider a simple model of an annual plant. Let $V(t)$ and $R(t)$ be the mass (in mg) of the vegetative and reproductive compartments, respectively, and let L be a constant which converts vegetative mass into photosynthetic surface area ($\text{cm}^2 \text{mg}^{-1}$). The net carbon assimilation rate $A(t)$ is given in units of $\text{mg cm}^2 \text{d}^{-1}$. Then the growth of these two compartments can be described by the following equations:

$$\frac{dV}{dt} = \alpha L A(t) V(t) [1-u(t)] \tag{1a}$$

$$\frac{dR}{dt} = \beta L A(t) V(t) u(t), \tag{1b}$$

subject to boundary conditions

$$V(0) = V_0 \quad (2a)$$

$$R(0) = 0, \quad (2b)$$

where α and β are efficiency constants $\in [0,1)$, and u is a control variable $\in (0,1)$ for all t .

To consider the effect of mortality, assume that plants in this population have an expectation of dying given by $\mu(t)$. The cumulative probability of survival to time t is then defined by

$$\frac{dl}{dt} = -\mu(t) l(t), \quad (3)$$

subject to the boundary condition

$$l(0) = 1. \quad (4)$$

Equation (3) assumes that $l(t)$ is a function of t only, but this assumption can be modified.

Analysis

An optimal schedule of growth and reproduction for this system is one which maximizes total annual seed-set, i.e.,

$$W(T) = \int_0^T \frac{dR}{dt} l(t) dt, \quad (5)$$

where T is the final time of the growing season. Maximization of $W(t)$ is a problem of choosing the fraction of new photosynthate, u , for all time t , which yields the optimal value for (5). Maximizing this integral is equivalent (Bryson & Ho 1975) to maximizing at every instant in time the scalar Hamiltonian function

$$H = \frac{dR}{dt} l(t) + \lambda(t) \frac{dV}{dt} \quad (6)$$

Here λ , the costate variable, is defined by

$$\frac{d\lambda}{dt} = -\frac{\partial H}{\partial V} = -L A(t) [\beta u(t) l(t) + \lambda(t) \alpha (1-u(t))] \quad (7)$$

and is subject to the boundary condition

$$\lambda(t) = 0. \quad (8)$$

We can find the optimal trajectory $\{u^*(t), V^*(t), R^*(t), \lambda^*(t); 0 \leq t \leq T\}$ using the methods of optimal control theory. For a maximum to exist at each point of the trajectory, it is necessary for the Hamiltonian to be maximal with respect to the control, i.e.,

$$\left. \frac{\partial H}{\partial u} \right|_{u(t) = u^*(t)} = 0. \quad (9)$$

Differentiating (6) gives

$$\frac{\partial H}{\partial u} = L A(t) V(t) [\beta l(t) - \alpha \lambda(t)]. \quad (10)$$

Restricting our attention to the case where $A(t) \neq 0$ (a reasonable restriction because the control problem disappears when there is no new photosynthate), we observe that the sign of (10) depends entirely on the sign of the term in brackets. For convenience we will refer to this term, a so-called *switching function*, as

$$\sigma(t) = \beta l(t) - \alpha \lambda(t). \quad (11)$$

Because the Hamiltonian (6) is linear in the control, (10) is independent of u . Pontryagin et al. (1962) showed that in this circumstance, when the Hamiltonian is also linear in the state variables (V and R in the present case) and the final time is fixed, the optimal control is "bang-bang:" either all the way on or all the way off. There is no other way for condition (9) to be met. In the present case then, $u^*(t)$ is determined simply by the signum function $\text{sgn}(\sigma)$:

$$\begin{aligned} \sigma(t) > 0, [\text{i.e., } \beta l(t) > \alpha \lambda(t)], u^*(t) &= 1; \\ \sigma(t) < 0, [\text{i.e., } \beta l(t) < \alpha \lambda(t)], u^*(t) &= 0. \end{aligned} \quad (12)$$

Note that (12) implies that the values of α and β may play an important role in determining the ease with which switches occur between purely vegetative and purely reproductive growth; this issue is examined in Appendix II.

When $\sigma(t) = 0$ (i.e., when $\sigma(t) = \dot{\sigma}(t) = 0$), the optimal control cannot be determined by Eq. (10); so-called "singular control" is said to exist. In such cases one uses higher order derivatives of H with respect to u , in which u does not vanish, to find an explicit expression for $u^*(t)$. In the present study no examples were encountered which required calculation of singular controls.

The full system to be solved is thus given by

$$\begin{aligned} \frac{dV}{dt} &= \alpha L A(t) V(t) [1-u(t)] , & V(0) &= V_0, \\ \frac{dR}{dt} &= \beta L A(t) V(t) u(t) , & R(0) &= 0, \\ \frac{dl}{dt} &= -\mu(t) l(t) , & l(0) &= 1, \text{ and} \\ \frac{d\lambda}{dt} &= -L A(t) [\beta u(t) l(t) + \lambda(t) \alpha (1-u(t))] , & \lambda(t) &= 0, \end{aligned} \tag{13}$$

subject to (12).

Since the costate variable, λ , plays an important role in determining switches from vegetative to reproductive growth, it is useful to discuss its

interpretation at this point. The costate variable here represents the gradient of fitness $W(t)$ (Eq. 5) with respect to variations in vegetative mass V ; equivalently one can think of λ as representing the marginal value of vegetative mass at each time t . This relationship can be seen intuitively by recalling that λ is uniquely defined in terms of changes in the Hamiltonian function -- which we are trying to maximize -- with respect to the state variable V (Eq. 7). Consequently λ declines monotonically until it is zero at the seasons' end -- vegetative structures at that time clearly have no residual value. An excellent intuitive discussion of costate variables is given in Iwasa and Roughgarden (1984).

Since (12) gives the conditions for optimal switches between vegetative and reproductive growth, we can use it to solve Eqs. (13) for the optimal life histories given a set of model parameters. This is not in general a simple task: boundary conditions on λ are imposed only at $t=T$, but the boundary conditions on l , R , and V are imposed at $t=0$. Equations (13) are thus a two-point boundary value problem. Solution of such problems often requires special numerical techniques.

In the present case, it is not particularly difficult to solve these equations because l and λ are independent of V and R . Since $\lambda(T)$ must = 0, and $l(t)$ can be found independently, we can integrate the equations for l and λ backward

from $t=T$ to find the optimal switching times, then use those solutions to integrate the state equations forward from $t=0$.

Numerical experiments

To examine the effects of variation in the survivorship curve, I initially used a smooth function for μ , and examined responses under four different survivorship regimes (fig. 4.1). I also considered arbitrary, non-smooth values for μ (fig. 4.1), similar to those reported in data sets from natural populations (e.g., Chapters 1,2).

To study the effects of variation in the net assimilation rate, I varied both the mean rate of net assimilation during a season, as well as within-season trends in the net assimilation rate. By representing the assimilation rate as the first n elements of a Fourier series

$$\text{(i.e., } A[t] = \frac{a_0}{2} + \sum_{i=1}^n \{ a_i \sin \frac{2i\pi t}{T} + b_i \cos \frac{2i\pi t}{T} \},$$

it was possible to vary these components of the assimilation rate independently.

Changes in the mean correspond to variation in the 0th order term, while within-season trends can be altered by varying higher order terms (fig. 4.2).

Using the conditions for optimal switching (12) I solved eqs. (13) under all combinations of these mortality and growth regimes.

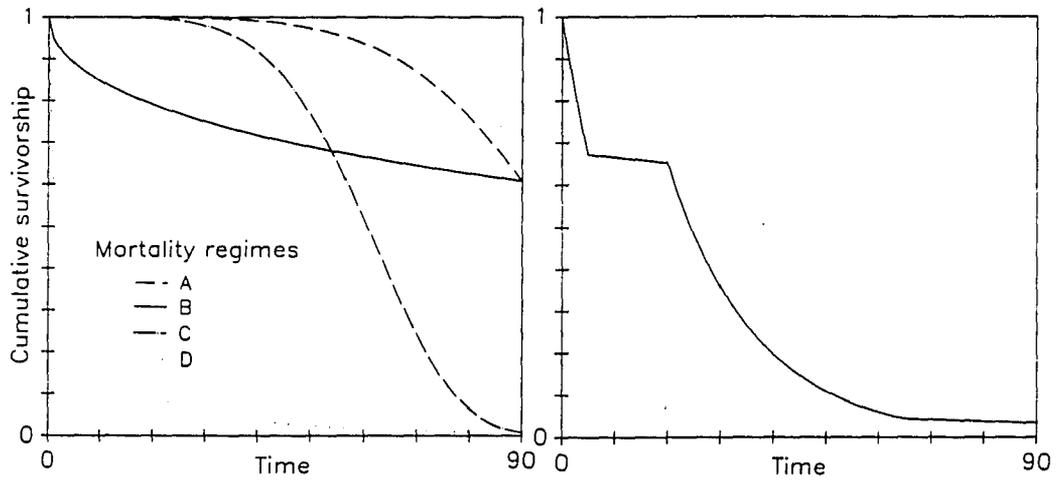


Fig. 4.1. Survivorship functions used in numerical analyses. A) Smooth survivorship functions. B) Arbitrary survivorship function.

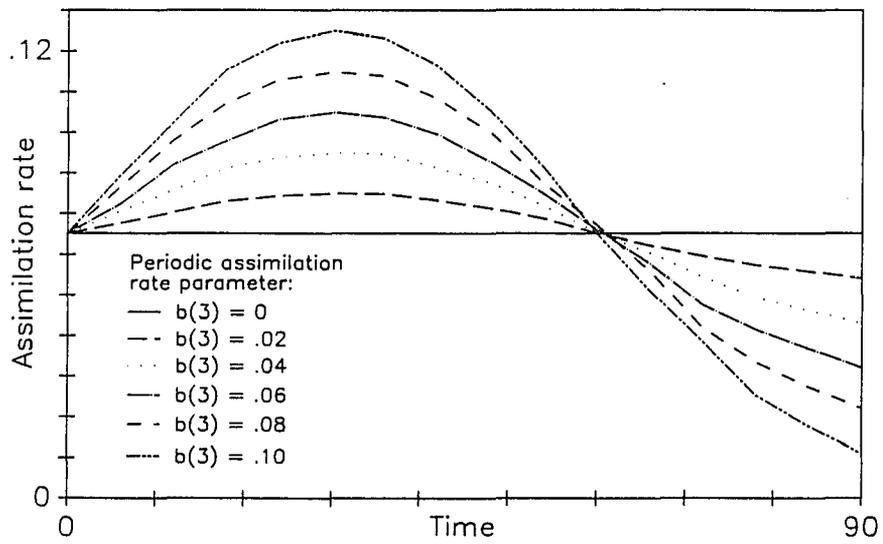


Fig. 4.2. Variation in seasonal trends in the assimilation rate $A(t)$. Areas under the curves are equal.

Open and closed loops

Before examining the results of these numerical experiments, it is important to consider the kinds of predictions these models can make. In varying growth and mortality regimes, are we predicting variation among populations, among individuals, or within individuals? Since solutions of optimal control problems can be interpreted as either "closed loop" (i.e., with feedback from the state variables) or "open loop" (no feedback) solutions, the answer depends not on the mathematics involved but on the relevant biology and the way it is represented in the model (Cruz 1972, Bryson & Ho 1975, Vincent & Pulliam 1980).

In varying mortality rates, we are making predictions about the mean behaviors of populations. This is because the model concerns the growth of an individual plant, but mortality rates are population-level phenomena. Since individuals do not experience mortality rates -- they can only be dead or alive at any particular moment -- the experimental variation of mortality rates can only lead to predictions about variation among populations. One could, of course, derive a model in which the plant assessed the present risk of mortality from its present state and acted accordingly, but it is not clear that doing so would be biologically reasonable.

In varying assimilation rates, however, we could be making predictions about mean behaviors of populations, or about how individuals should optimally respond to an unpredictable environment. Even in the absence of genetic variation, individuals within populations necessarily have different sequences of assimilation rates throughout their lives (hereafter, "assimilation trajectories"), since climate and microhabitat vary randomly. Responses to this variability could be of considerable selective importance; note that the optimal allocation schedule for the average assimilation trajectory will not generally be optimal for other conditions. Therefore it might be reasonable to interpret the present variation in assimilation rates as a "closed loop" solution to the model -- one which predicts an optimal phenotypic plasticity.

Results and discussion of numerical experiments

Variations in mean assimilation rate within a season

Increasing the average within-season assimilation rate uniformly delays the optimal date of first flowering (fig. 4.3). In general these delays in flowering are small, but lead to large differences in fitness $W(T)$ (fig.4.4). This is a consequence of the linear form of the present model and of bang-bang control: each compartment grows exponentially or not at all, and small variation in flowering time has a magnified effect on total reproductive output. Fitness --

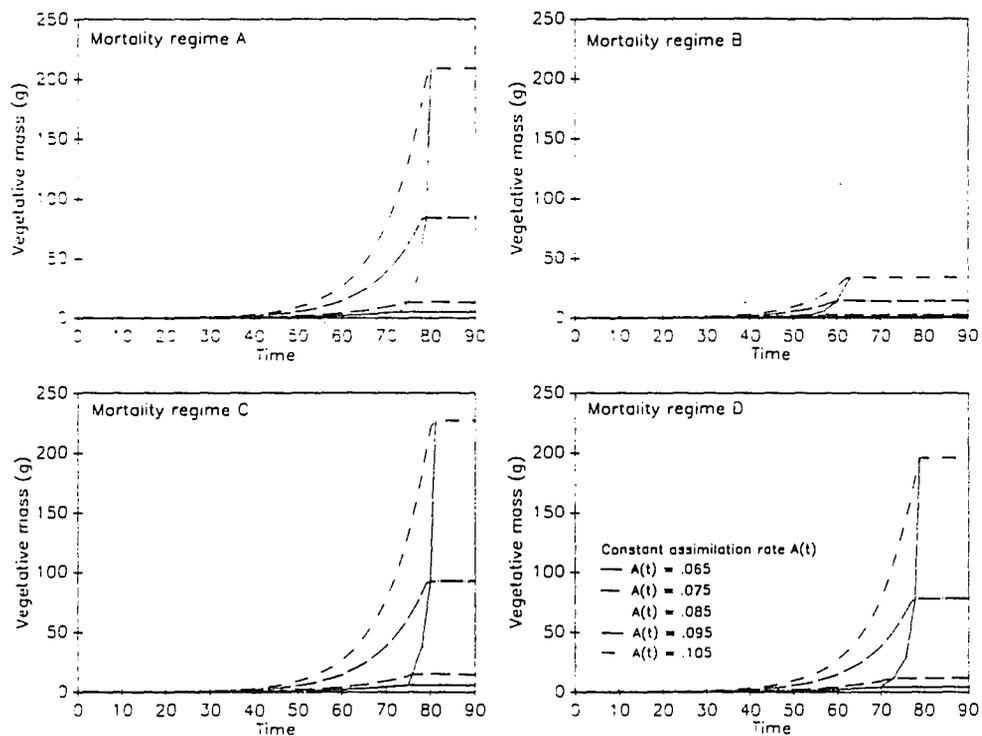


Fig. 4.3. Optimal trajectories for vegetative mass $V^*(t)$ when average assimilation rate is varied. Survivorship regimes as in fig. 1.

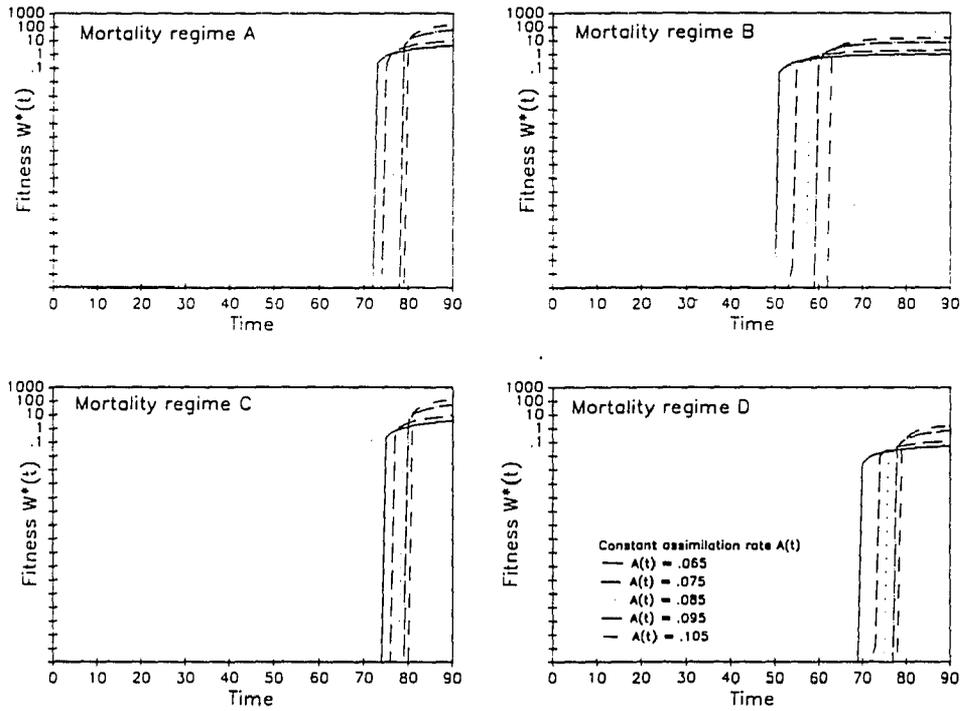


Fig. 4.4. Expected fitness $W^*(t)$ for optimal life histories when average assimilation rate is varied. Survivorship regimes as in fig. 1.

taken as expected reproductive output $W(t)$ throughout this chapter -- is therefore predicted to be most sensitive to departures from optimal allocation schedules when the mean assimilation rate is high (fig. 4.5).

Variation in within-season trends in assimilation rates

When net assimilation rates are high early in the season, it is optimal to begin flowering earlier. Variation in seasonal trends in the assimilation rates had strong effects on the optimal flowering time, t_s^* , only when the assimilation rate was nearly constant (fig. 4.6). But while the optimal flowering time varies little when there are strong within-season trends, the fitness consequences of flowering time are greatly magnified. Plants with early t_s^* -- those growing in environments with high assimilation rates early in the season but low assimilation rates late in the season -- produce much more reproductive tissue than do plants with later t_s^* (fig. 4.7). Moreover, sensitivity to non-optimal behavior is greater among these plants (fig. 4.8). These effects were present only with low mortality rates (figs. 4.6 - 4.8). At high mortality rates the switching curve is virtually a straight line (fig. 4.6).

Consequences of mortality: smooth survivorship curves

Not surprisingly, increases in mortality rate uniformly decrease the optimal date of first flowering, t_s^* (figs. 4.3, 4.6). These effects were fairly small for low

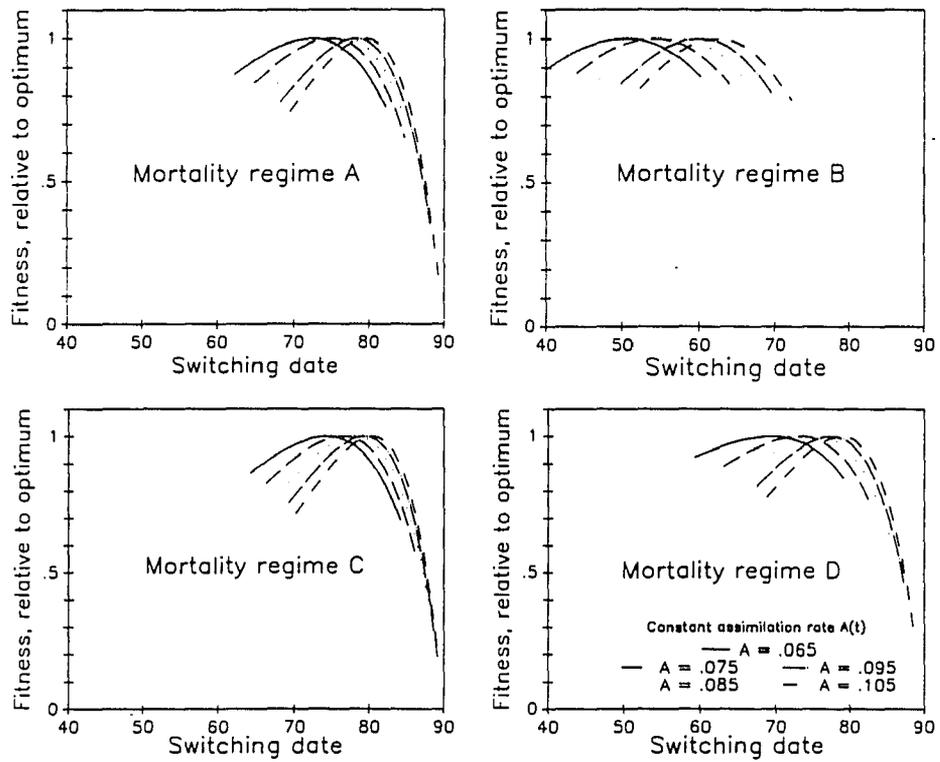


Fig. 4.5. Sensitivity analyses for the case of constant assimilation rates. Each curve shows the ratio $W(T)/W^*(T)$, as a function of flowering time t_s , for a plant experiencing a particular constant assimilation rate. Survivorship regimes as in fig. 1.

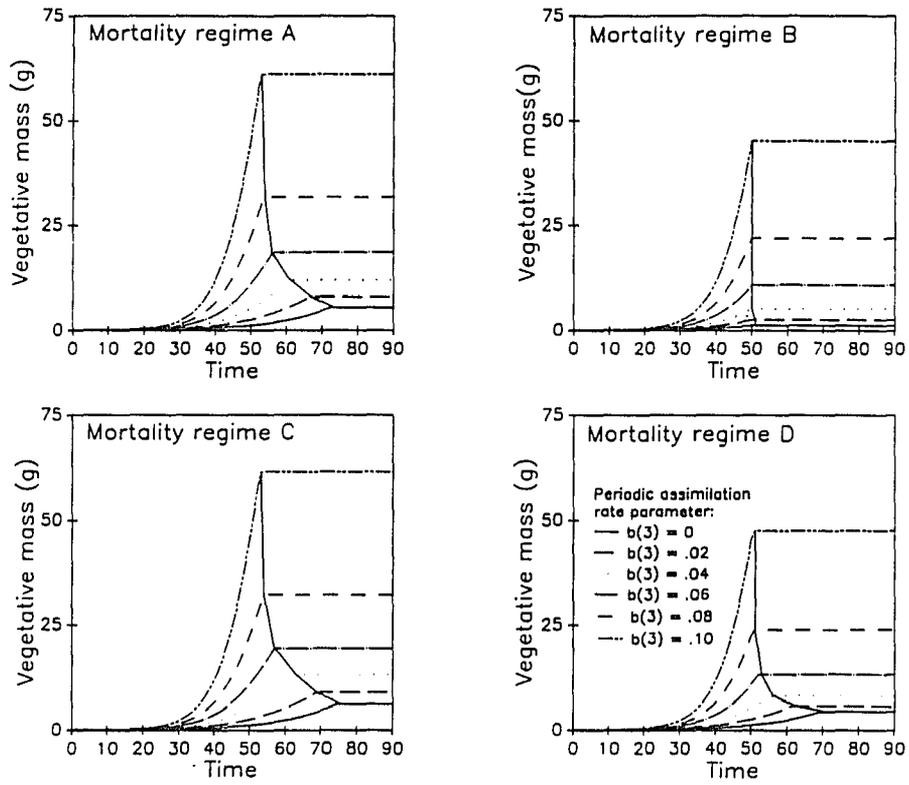


Fig. 4.6. Optimal trajectories for vegetative mass $V^*(t)$ when seasonal trends in assimilation rate are varied. Survivorship regimes as in fig. 1.

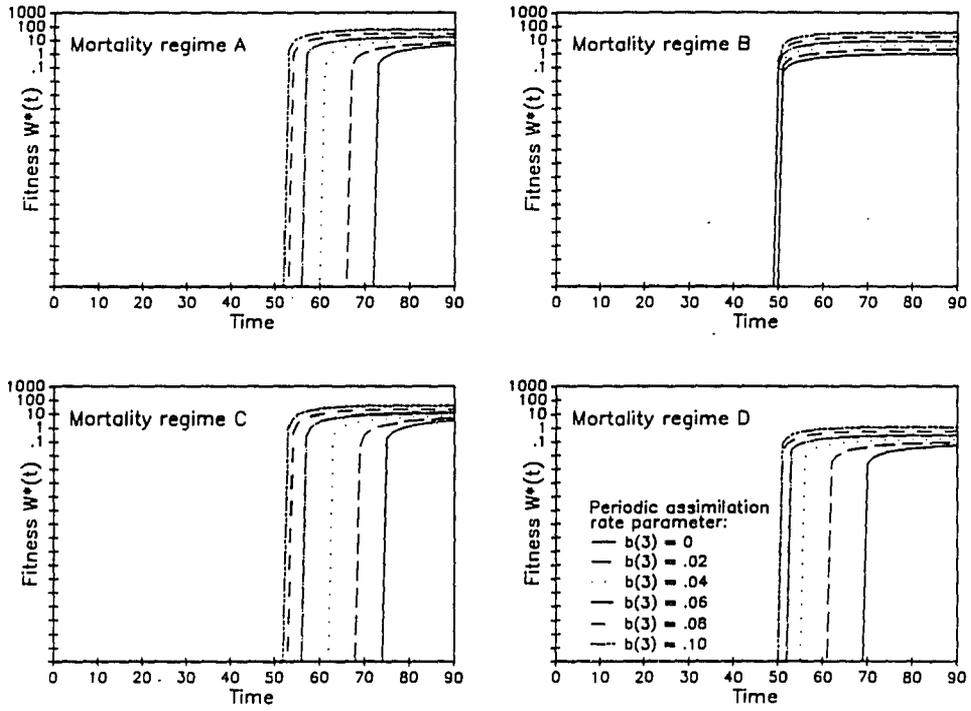


Fig. 4.7. Expected fitness $W^*(t)$ for optimal life histories when seasonal trends in assimilation rate are varied. Survivorship regimes as in fig. 1.

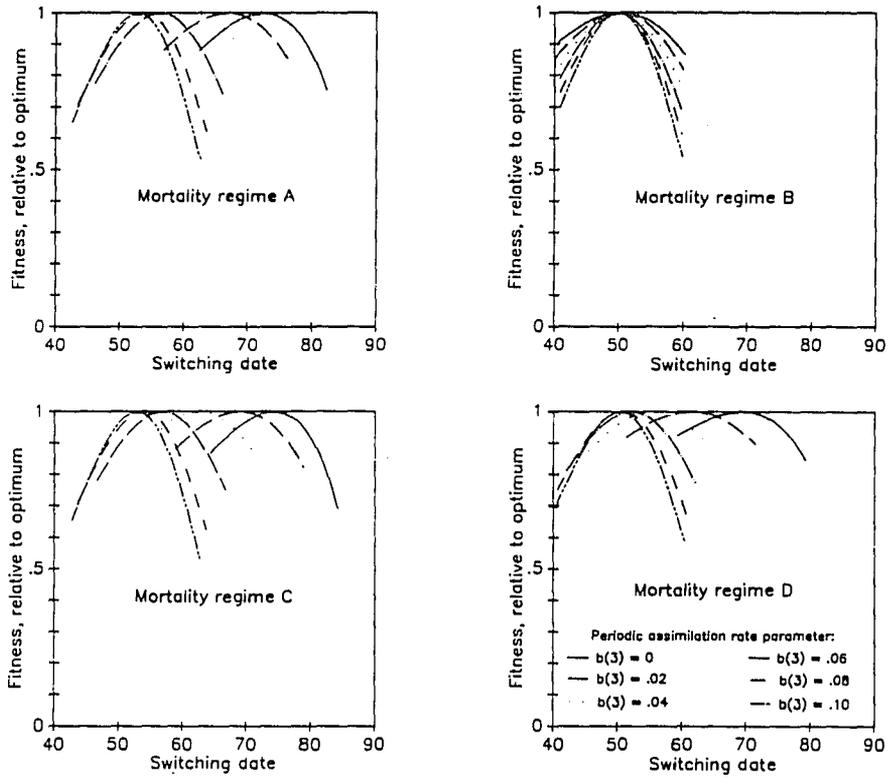


Fig. 4.8. Sensitivity analyses for variable assimilation rates. Each curve shows the ratio $W(T)/W^*(T)$, as a function of flowering time t_s , for a plant experiencing a particular assimilation trajectory (fig. 2). Survivorship regimes as in fig. 1.

mortality rates. Sensitivity to non-optimal behavior was much greater with low mortality rates (figs. 4.5, 4.8). With severe mortality rates, t_s^* varies little but the shape of the sensitivity curves change as one varies the seasonal trends in assimilation rates (figs. 4.5, 4.8). Optimal solutions exist in which the large majority of individuals die before t_s^* .

Multiple switches with arbitrary survivorship curves

As soon as one uses non-smooth functions for μ (fig. 4.1), it becomes easy to find optimal trajectories which include multiple episodes of flowering separated by periods of vegetative growth. King and Roughgarden (1982a) predicted multiple switches as an optimal strategy in response to variation in net assimilation rates within a season. In this study too, multiple switches depend partly on the mean assimilation rate experienced by the plant (fig. 4.9). This implies that, using a closed loop interpretation of the model, one could find populations in which multiple switches were optimal for one plant but not for its neighbor, which experiences a different microhabitat.

This could introduce some new difficulties in empirical work. For example, note that while each assimilation trajectory leads to a unique optimal life history, $R(t)$ is no longer unique where multiple switches exist; one could no longer infer anything about the individual's life history from this single measurement. The existence of multiple switches implies certain conditions on

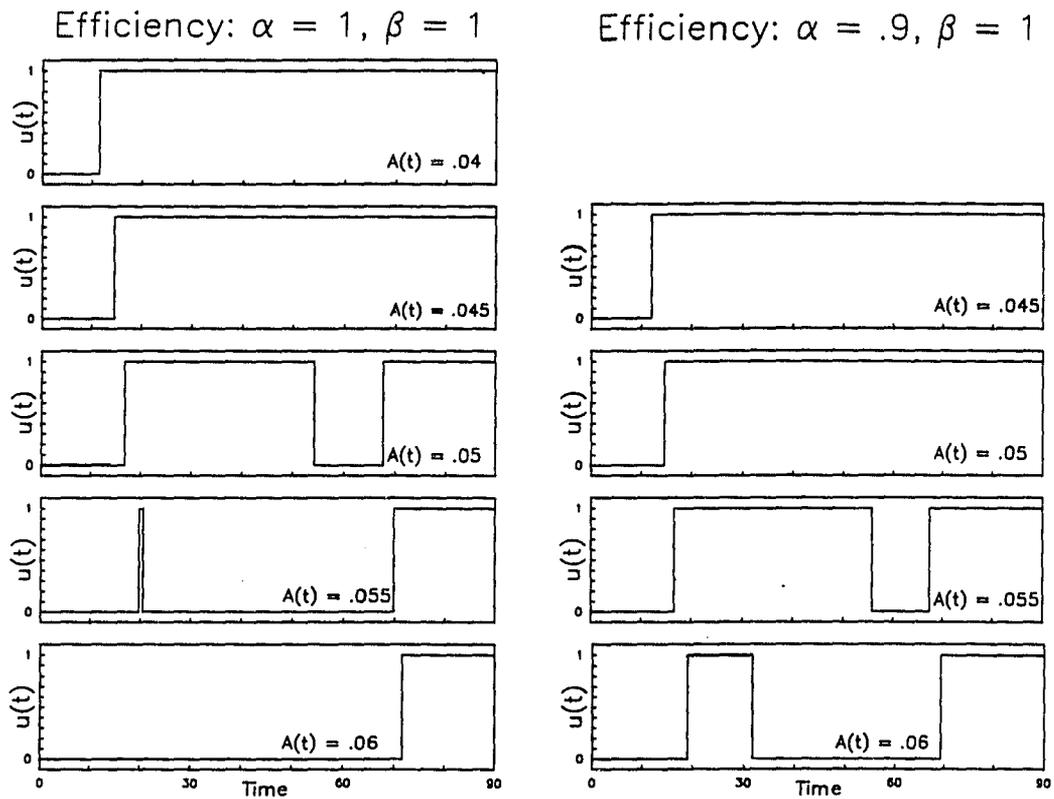


Fig. 4.9. Optimal trajectories for control variable $u^*(t)$ under arbitrary survivorship regime (fig. 1b), including multiple switches for some assimilation rates. Left, efficiency coefficients $\alpha = \beta = 1$. Trajectories for $A(t) = .085$ and $.095$ have multiple switches; the first flowering episode in the trajectory for $A(t) = .085$ lasts less than 0.5% of the season. Right, efficiency coefficients $\alpha = 0.9$, $\beta = 1$. Trajectory for $A(t) = .085$ no longer has a multiple switch, but that for $A(t) = .105$ now has multiple switches; switching is more stable. There is no longer an optimal solution for plants with $A(t) = .065$.

the values of σ and its time derivatives. In Appendix I, I show that these conditions can be used to examine the maximum number of switches which may exist in an optimal life history. In general such multiple switches depend not only on a_0 , but also on α and β ; this dependence is discussed in Appendix II.

III. Allometric constraints on carbon allocation

The model discussed above predicts that an annual plant growing in a season of fixed length should have an all-or-none flowering behavior; this result has been derived many times previously (Cohen 1971; Paltridge & Denholm 1974; Vincent & Pulliam 1980; Schaffer et al. 1982; Chiariello & Roughgarden 1984; Iwasa & Roughgarden 1984). However, there is a corollary of this prediction which immediately suggests a problem: for such plants the graph of $R(t) = f[V(t)]$ is a pair of straight lines with a single right-angle at t_s^* (for plants with a single switch; for multiple switches, the graph would have a stair-step shape). But real data sets generally show a curve with finite slope for such relationships (Rathcke & Lacey 1985; Samson & Werk 1986 and references therein; Fox unpubl. data).

Three hypotheses suggest themselves as possible explanations for this discrepancy. First, carbon allocation may be constrained, e.g., by developmental factors, in ways not permitting such bang-bang allocation. Second, seasons are generally of variable length; King and Roughgarden (1982) showed that under

such conditions a period of graded control ending in 100% allocation to reproduction was optimal. Third, plants may not behave optimally. I consider a model incorporating the first hypothesis.

A model

Consider a plant described by the same equations and boundary conditions as in the first model,

$$\frac{dV}{dt} = \alpha L A(t) V(t) [1-u(t)]$$

$$\frac{dR}{dt} = \beta L A(t) V(t) u(t)$$

$$\frac{dl}{dt} = -\mu(t) l(t)$$

$$V(0) = V_0$$

$$R(0) = 0,$$

$$l(0) = 1$$

(14)

Now assume that the relationship between $V(t)$ and $R(t)$ can be described by some allometric relationship, such that

$$R(t) = a + b V(t)^c.$$

(15)

Such a relationship could result from a variety of developmental or biophysical causes. In herbaceous plants, for example, lateral organs such as reproductive tissue and leaves are differentiated more or less periodically as a consequence of shoot extension. Equations such as (15) can therefore serve as phenomenological descriptions of the consequences of this underlying developmental process.

To treat this allometric relationship as a constraint, differentiate (15) to get

$$\frac{dR}{dt} = c b V^{(c-1)} \frac{dV}{dt}. \quad (16)$$

Substitution from (14) and rearrangement gives

$$A(t) V(t) u(t) - A(t) V(t)^c b c [1-u(t)] = 0, \quad (17)$$

which with further rearrangement yields the relationship

$$u(t) = \frac{c b V(t)^c}{V(t) + c b V(t)^c}. \quad (18)$$

Equation (18) gives the value which u must take during flowering, in order to satisfy (15) for some value of the intercept a . Note that for $c = 1$, u becomes a constant. It may be a more common allometric relation, however, to

have $c < 1$; in this case, Eq. (18) implies a monotonic decline in u , following the initiation of flowering. This formulation thus predicts something new for plants with allometric growth constraints: allocation to reproduction may decline with time. We can treat (18) as an explicit constraint by first defining (Bryson & Ho 1975)

$$S(t) = \frac{c b V(t)^c}{V(t) + c b V(t)^c} - u(t). \quad (19)$$

Note that $S(t) \geq 0$ for all t .

Analysis

We can now define the Hamiltonian,

$$H = \frac{dR}{dt} l(t) + \lambda(t) \frac{dV}{dt} + \phi(t) S(t), \quad (20)$$

where ϕ is a Lagrange multiplier chosen to satisfy the condition

$$\frac{\partial H}{\partial u} \bigg|_{u(t)=u^*(t)} = 0. \quad (21)$$

and λ is again the costate variable. The Lagrange multiplier ϕ is analogous to the costate variable λ in that it can be interpreted as the marginal cost of the

constraint or as the gradient of fitness $W(t)$ with respect to the constraint; however, ϕ is defined in a static sense.

It simplifies matters in this case to consider the values of ϕ which satisfy (21) before writing the equation for λ . Differentiating (20) with respect to u gives

$$\frac{\partial H}{\partial u} = \sigma(t) = L A(t) V(t) [\beta l(t) - \alpha \lambda(t)] - \phi(t). \quad (22)$$

Note that in this case $\text{sgn} \left(\frac{\partial H}{\partial u} \right)$ is determined by (22) as a whole.

Condition (21) can therefore be met by choosing

$$\phi(t) = \begin{cases} 0, & S(t) > 0 \\ L A(t) V(t) [\beta l(t) - \alpha \lambda(t)], & S(t)=0. \end{cases} \quad (23)$$

Since the Hamiltonian is linear in control and state variables and the final time is fixed, the optimal control is still bang-bang. However, "bang-bang" should be understood as "fully saturated;" when flowering the plant optimally devotes the maximum amount of carbon possible (now defined by (18) rather than as 100%). Thus

$$u(t)^* = \begin{cases} 0, & \sigma(t) < 0 \\ \frac{c b V(t)^c}{V(t) + c b V(t)^c}, & \sigma(t) > 0. \end{cases} \quad (24)$$

As a consequence, (23) is equivalent to

$$\phi(t) = \begin{cases} 0, & u(t) = 0 \\ L A(t) V(t) [\beta I(t) - \alpha \lambda(t)], \\ \\ u(t) = \frac{c b V(t)^c}{V(t) + c b V(t)^c}. \end{cases} \quad (25)$$

Using (23-24) we can write the equation for λ as

$$\begin{aligned} \frac{d\lambda}{dt} = - \frac{\partial H}{\partial V} = & - L A(t) \{ I(t) u(t) \beta + \lambda(t) [1-u(t)] \alpha \\ & + \phi(t) \frac{c b V(t)^c (c-1)}{[V(t) + c b V(t)^c]^2} \}, \end{aligned}$$

when $S(t) = 0$, $u(t) \neq 0$,

and

$$\frac{d\lambda}{dt} = - L A(t) \lambda(t) \alpha,$$

when $S(t) > 0$, $u(t) = 0$. (26)

Numerical analysis

To examine the consequences of variation in the allometric exponent c , I solved Eqs. (14,23,26) subject to (25), for values of c between 1 and 0.5. The mortality regime used is shown in fig. 4.1; the assimilation rate A was not varied. Numerical solution of this two-point boundary value problem requires use of a shooting method.

Since we are examining the consequences of a constraint, the family of solutions for varied c should be understood as predictions about variation among individuals or populations, not as closed loop solutions predicting optimal phenotypic plasticity.

All of the examples studied involved a single switch as the optimal solution (fig. 4.10). Decreasing the allometric exponent c from 1 leads to earlier t_s^* (fig. 4.10). This makes intuitive sense: plants constrained to devote fewer resources to reproduction can partly compensate with an earlier onset of flowering. While plants on different optimal paths differ in t_s^* , these differences are fairly small; the major consequences of varying c on optimal allocation schedules are on $R(t)$ and fitness $W(t)$. Trajectories for V cross for plants with different values of c . Thus measurements of size at a point in time do not uniquely identify the trajectories of these plants.

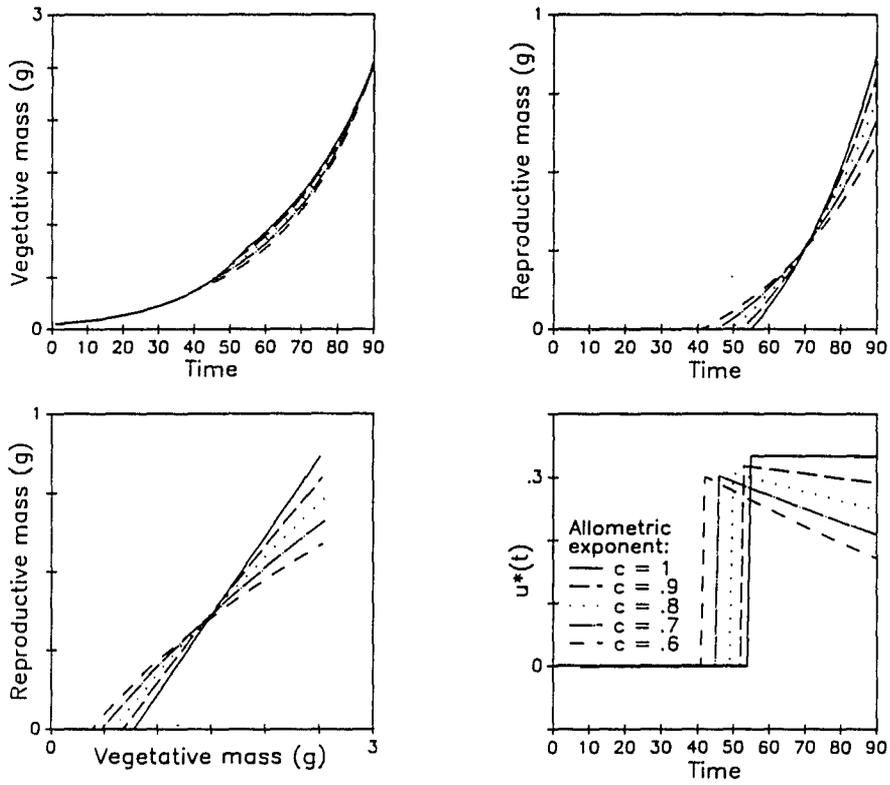


Fig. 4.10. Optimal trajectories under allometric growth constraints; allometric exponent c varied from 1 to 0.6. A) Vegetative mass $V^*(t)$. B) Reproductive mass $R^*(t)$. C) Reproductive mass $R^*(t)$ as a function of vegetative mass $V^*(t)$. D) Control variable $u^*(t)$.

IV. Discussion

Mortality

It is not difficult to incorporate the risk of mortality in models of optimal carbon allocation. It is frequently assumed (e.g., Rathcke & Lacey 1985, Lacey 1986) that annual plants are so plastic that they can generally set seed before dying, but extensive empirical evidence suggests otherwise (e.g., Tevis 1958a, 1958b; Beatley 1967; Loria & Noy-Meir 1979-80; Inouye 1980; Burk 1982; D.L. Venable, unpubl. data; see also chapters 1 and 2). It seems reasonable to suggest that the risk of mortality may be a major selective force acting on schedules of resource allocation for annual plants.

This conclusion is similar to those reached by Kozłowski and Wiegert (1986) for annual organisms reproducing continuously or in repeated clutches during the growing season. On the other hand, these authors concluded that mortality does not affect the optimal time for reproduction in organisms releasing stored reproductive energy in an instantaneous burst at the end of the season ("semelparity" in their terminology), and argued that this result justifies neglecting within-season mortality. I suggest that such a conclusion is unwarranted for at least three reasons. First, continuous reproduction or reproduction in repeated clutches throughout the growing season characterizes most annual plants and many annual insects. Second, the definition of

"semelparity" used by Kozłowski and Wiegert (1986) to reach this conclusion requires that reproduction be literally instantaneous, immediately prior to the end of the season (see their fig. 2A); if reproduction takes finite time, their conclusion no longer holds. Finally, it seems clear that, even in organisms reproducing instantaneously at the end of the season, the probability of survivorship to reproduction may strongly affect the existence of an optimal solution, regardless of its effects on the value of such optima.

So long as one assumes that the risk of mortality varies smoothly over time, the effect of mortality on the optimal life history is not surprising: the optimal date of first flowering, t_s^* , is earlier in plants more likely to die. This is not an insubstantial effect if one wishes to make testable predictions.

As soon as one incorporates risks of mortality which can vary abruptly -- such as those found in real data sets -- the situation changes: one can easily find optimal solutions involving multiple episodes of flowering. In general these depend on the efficiency coefficients α and β (appendix II), suggesting that it may be necessary to estimate such quantities in order to assess even the qualitative fit of the model to any real data set. Mortality regimes can thus qualitatively change the optimal life history.

The mortality regimes used in the present chapter are functions of time only. It is undoubtedly more realistic to treat the risk of mortality as a function

of time and the state of the plant, and the models used here can easily be extended to do so. A meaningful extension in this direction would, however, require substantial detail about the relationship between the risk of mortality and the plant's status -- a relationship which has not yet been elaborated for any plant species. Moreover it is not clear whether state-dependent mortality risks really affect the allocation schedules of any species.

Constraints on carbon allocation

Most previous treatments of optimal schedules of carbon allocation in annual plants have assumed that the control variable u is a free parameter. Together with other assumptions -- the state equations written to yield a Hamiltonian linear in control and state variables, and length of the season fixed -- this assumption leads to the prediction that u should take on only two values, 0 and 1. As noted above, this would lead one to expect a graph of $R(t) = f[V(t)]$ which is two straight lines joined by a right angle at $t = t_s^*$. Instead we find graphs of varying kinds, but all have finite slope during the reproductive period, and many are declining curves.

In most herbaceous plants both leaves and reproductive organs are differentiated from meristematic tissue only as a consequence of axis extension (Bernier 1966, Esau 1977, King 1981, Green & Poethig 1982). Production of leaves is often stopped or limited to production of bracts after onset of flowering

-- but V continues to increase because of the addition of stem tissue. It thus appears inappropriate to assume that it is possible in most plants for u to take on arbitrary values on the interval (0,1); resource allocation appears to be highly constrained.

I have treated the underlying developmental processes as an allometric growth constraint in the present chapter. At a fine level of resolution this approximation would fail since lateral organs -- leaves and reproductive organs -- are differentiated more or less periodically. At the moment, testing models at such a fine level of resolution is clearly impossible, so the approximation might be a useful one. Alternatively one could directly model the growth of the apical dome and differentiation of lateral organs (Charles-Edwards et al. 1979).

A recent study by Kozłowski and Ziólko (1988) also addresses the problem of developmental constraint. These authors examined the optimal life history for organisms in which the young reproductive organs cannot use all of the carbon produced by the vegetative organs because of their initially small size. Using a more general mathematical approach, these authors conclude that, for organisms with this kind of growth constraint, the optimal life history is divided into three intervals: vegetative growth, mixed growth, and 100% reproduction. Their conclusion differs from mine only because of the different kinds of growth constraints examined. In the case considered here -- herbaceous plants -- the

reproductive primordia must be initiated repeatedly as the plant grows; hence the phase of 100% reproductive allocation is not reachable.

How bright a future?

If we make the assumption that natural selection results in life histories which are close to their optima, we can uniquely predict plants' carbon allocation schedules. There are, however, substantial difficulties in proceeding from this assumption to meaningful empirical tests of such models.

Results of sensitivity analyses suggest that departures from optimal flowering time have the greatest consequences in plants with very low mortality rates and those with initially high but subsequently declining assimilation rates. One could therefore expect that selection for optimal allocation schedules is strongest -- and therefore that natural populations might display the least scatter -- under such circumstances. Ironically, low mortality rates are not characteristic of many populations of annual plants, although seasonal variation in assimilation rates probably does characterize most annual populations.

Many of the analyses predict little variation in such readily measurable characters as time of first flowering, but substantial variation in fitness. It is difficult at best to measure fitness in the sense of $W(t)$ since it involves some quantities which can be measured only at the individual level and others which are population-level properties. Worse still, several analyses suggest that one

could tell whether a plant is performing optimally only with knowledge of its entire life history.

While one could in principle use closed loop solutions of optimal control problems to predict optimal patterns of phenotypic plasticity, the qualitative pattern predicted above -- delays in flowering in response to suppressed assimilation rates early in life -- also appears to be an unavoidable consequence of water stress in many annual plants (chapter 2). To test whether an observation is an optimal plasticity or an unavoidable response, one would therefore need to consider quantitative predictions. Similarly, testing whether the observed scatter in flowering time is an optimal plasticity would require continuous measurement of the assimilation rates of individual plants.

Since there are difficulties in evaluating the quantitative predictions of these models, it makes sense to ask: is it possible to derive unambiguous and testable qualitative predictions? The present analysis suggest that this may not be the case. For example, the number of switches in an optimal life history may depend sensitively on values of the parameters α and β and on the assimilation trajectory experienced by an individual plant (appendix II). Other qualitative predictions -- e.g., that annual plants begin life with a phase of purely vegetative growth but subsequently begin to flower -- hardly require the machinery of optimal control theory!

The seemingly cloudy future for empirical tests of optimal control models of annual plant life histories does not necessarily imply a cloudy future for understanding life history evolution. As I noted in the introduction, the optimal control approach represented a conceptual advance because it considers the organisms' entire life history. Many of the ambiguities which one might encounter in applying these models to experimental or field situations are ambiguities precisely because they require knowledge of the entire life history. This suggests that attempts to consider the adaptive significance at this level of variation -- where phenotypic differences are, by definition, fairly small -- may require a basis in the mechanisms underlying life histories.

Appendix I: Conditions under which multiple switches may occur

Optimal switching behavior can be viewed as a function of the time derivatives of the switching function σ . I consider here the case where u may take any value on the interval $(0,1)$.

By definition, if an optimal solution exists $\sigma(0) < 0$ and $\sigma(t) > 0$; consequently $u^*(0) = 0$, and $u^*(t) = 1$. This leads to the conclusion reached by King and Roughgarden (1982a), that in an optimal life history, the number of switches is odd.

In general, the signum function $\text{sgn}(\dot{\sigma})$ sets a limit on the maximum number of switches possible in an optimal life history, where the dot notation indicates a derivative with respect to time. This is because an optimal solution, if it exists, includes at least a single switch, requiring at least a single time interval in which the time derivative of $\sigma > 0$. Similarly, if the optimal life history involves multiple switches, there is at least one interval in which $\text{sgn}(\dot{\sigma}) < 0$ prior to each switch from flowering to vegetative growth.

These properties of optimal life histories prove the following result:

Result: In an optimal life history with n switches (n odd),

at least $1 + \frac{n-1}{2}$ intervals must occur with

with $\dot{\sigma}(t) > 0$, and at least $\frac{n-1}{2}$ intervals must

occur with $\dot{\sigma}(t) < 0$.

This result implies two corollaries:

Corollary 1: In an optimal life history with n switches (n odd and > 1)

there must be at least $(n - 1)/2$ intervals with $\ddot{\sigma}(t) > 0$ and

the same number of intervals with $\ddot{\sigma}(t) < 0$.

Corollary 2: In an optimal life history with n switches (n odd and > 1)

there must be at least $n - 2$ inflection points in the switching

function $\sigma(t)$.

Appendix II: Effects of efficiency coefficients

Analysis of the effects of values of the efficiency coefficients α and β (eq. 13) follows from appendix I. To consider the effects of these parameters on switching behavior, begin by taking the time derivative of the switching function (11):

$$\dot{\sigma} = \begin{cases} \beta l(t) [\alpha L A(t) - \mu(t)], & u(t) = 1 \\ \alpha^2 L A(t) \lambda(t) - \beta l(t) \mu(t), & u(t) = 0 \end{cases} \quad (\text{AII.1})$$

During flowering the sign of (AII.1) can change depending on changes in the values of A and μ . During vegetative growth changes in λ and l can also lead to sign changes in (AII.1); this is in fact inevitable if an optimal solution exists, since λ and l decline monotonically. Also note that sign changes can occur more easily when α is large.

To further examine how the coefficients α and β affect switching behavior, differentiate (AII.1) to get

$$\begin{aligned} \frac{d\dot{\sigma}}{dp} &= \begin{cases} L \beta A(t) l(t) \\ - l(t) [\mu(t) - L \alpha A(t)] \end{cases}, & u(t) = 1, \\ \text{and} \\ \frac{d\dot{\sigma}}{dp} &= \begin{cases} 2\alpha L A(t) \lambda(t) \\ - l(t) \mu(t) = \dot{l}(t) \end{cases}, & u(t) = 0, \end{aligned} \quad (\text{AII.2})$$

where \mathbf{p} is a parameter vector with $p_1 = \alpha$ and $p_2 = \beta$.

Note that the derivative with respect to α is always positive. Increasing α (i.e., increasing the efficiency of vegetative growth) thus always increases the slope of $\dot{\sigma}$ -- changes in the switching function, including sign changes, may occur more suddenly. On the other hand, the derivative with respect to β is always negative when $u = 0$, but its sign depends on other variables when $u = 1$.

Differentiating again for the case of constant assimilation rate results in

$$\frac{d\ddot{\sigma}}{d\beta} = \begin{cases} -L \beta A(t) l(t) \mu(t) \\ l(t) \{ \alpha L A(t) [1 - \mu(t)] + \mu(t)^2 - \dot{\mu}(t) \} \end{cases}, u(t)=1,$$

and

$$\frac{d\ddot{\sigma}}{d\beta} = \begin{cases} -2 [\alpha L A(t)]^2 \lambda(t) \\ l(t) [\mu(t)^2 - \dot{\mu}(t)] \end{cases}, u(t) = 0. \quad (\text{AII.3})$$

The second derivative with respect to α is always negative. This indicates that increases in efficiency of vegetative growth always increase the curvature of the switching function, thus making switches more likely to occur. The effects of increasing β again depend on other terms.

APPENDIX

Complete Life Tables
for Organ Pipe and Portal Populations, 1985-1986

Table A1. Life table estimates and standard errors, Organ Pipe 1986.

| X | Dx | Wx | Nx | qx (SE) | lx (SE) | PDF (SE) | HAZ (SE) | ex (SE) |
|---|-----|----|-------|-----------|-----------|---------------|---------------|-------------|
| <u>A) 1-2cm Spring-Flowerers(B^{***},C^{***},G[*],H^{***})</u> | | | | | | | | |
| 0 | 2 | 0 | 78.0 | 0.03 0.02 | 1.00 0.00 | 0.0005 0.0004 | 0.0005 0.0004 | 78.46 3.40 |
| 50 | 65 | 0 | 76.0 | 0.86 0.04 | 0.97 0.02 | 0.0167 0.0008 | 0.0299 0.0025 | 29.23 3.35 |
| 100 | 9 | 0 | 11.0 | 0.82 0.12 | 0.14 0.04 | 0.0023 0.0007 | 0.0277 0.0067 | 30.55 9.21 |
| 150 | 1 | 0 | 2.0 | 0.50 0.35 | 0.03 0.02 | 0.0003 0.0003 | 0.0133 0.0126 | 50.00 35.36 |
| 200 | 0 | 0 | 1.0 | 0.00 -.- | 0.01 0.01 | 0.0000 -.- | 0.0000 -.- | -.- -.- |
| 250 | 1 | 0 | 1.0 | 1.00 -.- | 0.01 0.01 | 0.0003 0.0003 | 0.0400 0.0000 | -.- -.- |
| <u>B) 1 cm Non-Spring-Flowerers (A^{***},C^{***},D^{***},E^{***},F^{***},G^{***},H^{***},I^{***})</u> | | | | | | | | |
| 0 | 159 | 0 | 302.0 | 0.53 0.03 | 1.00 0.00 | 0.0105 0.0006 | 0.0143 0.0011 | 47.48 2.73 |
| 50 | 141 | 0 | 143.0 | 0.99 0.01 | 0.47 0.03 | 0.0093 0.0006 | 0.0389 0.0008 | 25.35 2.12 |
| 100 | 2 | 0 | 2.0 | 1.00 -.- | 0.01 0.00 | 0.0001 0.0001 | 0.0400 0.0000 | -.- -.- |
| <u>C) 2 cm Non-Spring-Flowerers (A^{***},B^{***},D^{***},E^{***},F^{***},G^{***},H^{***},I⁺)</u> | | | | | | | | |
| 0 | 92 | 0 | 539.0 | 0.17 0.02 | 1.00 0.00 | 0.0034 0.0003 | 0.0037 0.0004 | 71.16 1.38 |
| 50 | 419 | 1 | 446.5 | 0.94 0.01 | 0.83 0.02 | 0.0156 0.0004 | 0.0354 0.0008 | 26.64 1.26 |
| 100 | 26 | 0 | 27.0 | 0.96 0.04 | 0.05 0.01 | 0.0010 0.0002 | 0.0371 0.0027 | 25.96 5.00 |
| 150 | 1 | 0 | 1.0 | 1.00 -.- | 0.00 0.00 | 0.0000 0.0000 | 0.0400 0.0000 | -.- -.- |

Table A1, cont'd

| X | Dx | Wx | Nx | qx (SE) | lx (SE) | PDF (SE) | HAZ (SE) | ex (SE) |
|--|-----|----|-------|-----------|-----------|---------------|---------------|--------------|
| <u>D) 3 cm Spring-Flowerers (B^{***},C^{***},E⁺,H^{***})</u> | | | | | | | | |
| 0 | 11 | 0 | 135.0 | 0.08 0.02 | 1.00 0.00 | 0.0016 0.0005 | 0.0017 0.0005 | 80.71 3.16 |
| 50 | 92 | 0 | 124.0 | 0.74 0.04 | 0.92 0.02 | 0.0136 0.0008 | 0.0236 0.0020 | 33.70 3.03 |
| 100 | 22 | 0 | 32.0 | 0.69 0.08 | 0.24 0.04 | 0.0033 0.0006 | 0.0210 0.0038 | 36.36 6.43 |
| 150 | 3 | 0 | 10.0 | 0.30 0.14 | 0.07 0.02 | 0.0004 0.0003 | 0.0071 0.0040 | 125.00 19.76 |
| 200 | 0 | 0 | 7.0 | 0.00 -.- | 0.05 0.02 | 0.0000 -.- | 0.0000 -.- | 93.75 16.54 |
| 250 | 4 | 0 | 7.0 | 0.57 0.19 | 0.05 0.02 | 0.0006 0.0003 | 0.0160 0.0073 | 46.75 16.54 |
| 300 | 1 | 0 | 3.0 | 0.33 0.27 | 0.02 0.01 | 0.0002 0.0002 | 0.0080 0.0078 | -.- -.- |
| 350 | 2 | 0 | 2.0 | 1.00 -.- | 0.01 0.01 | 0.0003 0.0002 | 0.0400 0.0000 | -.- -.- |
| <u>E) 3 cm Non-Spring-Flowerers (B^{***},C^{***},G^{**},H^{***})</u> | | | | | | | | |
| 0 | 26 | 0 | 188.0 | 0.14 0.03 | 1.00 0.00 | 0.0028 0.0005 | 0.0030 0.0006 | 75.19 2.54 |
| 50 | 135 | 0 | 162.0 | 0.83 0.03 | 0.86 0.03 | 0.0144 0.0007 | 0.0286 0.0017 | 30.00 2.36 |
| 100 | 18 | 0 | 27.0 | 0.67 0.09 | 0.14 0.03 | 0.0019 0.0004 | 0.0200 0.0041 | 37.50 7.22 |
| 150 | 2 | 0 | 9.0 | 0.22 0.14 | 0.04 0.02 | 0.0002 0.0002 | 0.0050 0.0035 | 120.83 12.50 |
| 200 | 0 | 0 | 7.0 | 0.00 -.- | 0.04 0.01 | 0.0000 -.- | 0.0000 -.- | 79.17 11.02 |
| 250 | 6 | 0 | 7.0 | 0.86 0.13 | 0.04 0.01 | 0.0006 0.0003 | 0.0300 0.0081 | 29.17 11.02 |
| 300 | 0 | 0 | 1.0 | 0.00 -.- | 0.01 0.01 | 0.0000 -.- | 0.0000 -.- | -.- -.- |
| 350 | 1 | 0 | 1.0 | 1.00 -.- | 0.01 0.01 | 0.0001 0.0001 | 0.0400 0.0000 | -.- -.- |

Table A1, cont'd

| X | Dx | Wx | Nx | qx (SE) | lx (SE) | PDF (SE) | HAZ (SE) | ex (SE) |
|--|----|----|------|-----------|-----------|---------------|---------------|-------------|
| <u>F) 4-6 cm Non-Spring-Flowerers (B**,C***,H**)</u> | | | | | | | | |
| 0 | 4 | 0 | 29.0 | 0.14 0.06 | 1.00 0.00 | 0.0028 0.0013 | 0.0030 0.0015 | 79.17 748 |
| 50 | 18 | 0 | 25.0 | 0.72 0.09 | 0.86 0.06 | 0.0124 0.0018 | 0.0225 0.0044 | 34.72 694 |
| 100 | 5 | 0 | 7.0 | 0.71 0.17 | 0.24 0.08 | 0.0034 0.0014 | 0.0222 0.0083 | 35.00 1323 |
| 150 | 0 | 0 | 2.0 | 0.00 --- | 0.07 0.04 | 0.0000 --- | 0.0000 --- | 200.00 3536 |
| 200 | 0 | 0 | 2.0 | 0.00 --- | 0.07 0.04 | 0.0000 --- | 0.0000 --- | 150.00 3536 |
| 250 | 0 | 0 | 2.0 | 0.00 --- | 0.07 0.04 | 0.0000 --- | 0.0000 --- | 100.00 3536 |
| 300 | 1 | 0 | 2.0 | 0.50 0.35 | 0.07 0.04 | 0.0007 0.0007 | 0.0133 0.0126 | 50.00 3536 |
| 350 | 1 | 0 | 1.0 | 1.00 --- | 0.03 0.03 | 0.0007 0.0070 | 0.0400 0.0000 | --- --- |
| <u>G) 4 cm Spring-Flowerers (A*,B***,C***,E**,H*,I+)</u> | | | | | | | | |
| 0 | 3 | 0 | 64.0 | 0.04 0.03 | 1.00 0.00 | 0.0009 0.0005 | 0.0010 0.0006 | 83.72 465 |
| 50 | 43 | 0 | 61.0 | 0.70 0.06 | 0.95 0.03 | 0.0134 0.0012 | 0.0218 0.0028 | 35.47 454 |
| 100 | 10 | 0 | 18.0 | 0.56 0.12 | 0.28 0.06 | 0.0031 0.0009 | 0.0154 0.0045 | 45.00 1061 |
| 150 | 2 | 0 | 8.0 | 0.25 0.15 | 0.13 0.04 | 0.0006 0.0004 | 0.0057 0.0040 | 125.00 1768 |
| 200 | 0 | 0 | 6.0 | 0.00 --- | 0.09 0.04 | 0.0000 --- | 0.0000 --- | 87.50 1531 |
| 250 | 4 | 0 | 6.0 | 0.67 0.19 | 0.09 0.04 | 0.0013 0.0006 | 0.0200 0.0087 | 37.50 1531 |
| 300 | 0 | 0 | 2.0 | 0.00 --- | 0.03 0.02 | 0.0000 --- | 0.0000 --- | --- --- |
| 350 | 2 | 0 | 2.0 | 1.00 --- | 0.03 0.02 | 0.0006 0.0004 | 0.0400 0.0000 | --- --- |

Table A1, cont'd

| X | Dx | Wx | Nx | qx (SE) | lx (SE) | PDF (SE) | HAZ (SE) | ex (SE) |
|--|----|----|------|-----------|-----------|---------------|---------------|--------------|
| <u>H) 5-10 cm Spring Flowerers (A^{***},B^{***},C^{***},D^{***},E^{***},F^{**},G[*],I^{**})</u> | | | | | | | | |
| 0 | 3 | 0 | 44.0 | 0.07 0.04 | 1.00 0.00 | 0.0014 0.0008 | 0.0014 0.0008 | 107.69 12.76 |
| 50 | 17 | 0 | 41.0 | 0.41 0.08 | 0.93 0.04 | 0.0077 0.0015 | 0.0105 0.0024 | 63.46 12.31 |
| 100 | 13 | 0 | 24.0 | 0.54 0.10 | 0.54 0.08 | 0.0059 0.0014 | 0.0149 0.0038 | 46.15 9.42 |
| 150 | 4 | 0 | 11.0 | 0.36 0.14 | 0.25 0.07 | 0.0018 0.0009 | 0.0089 0.0043 | 115.00 16.58 |
| 200 | 0 | 0 | 7.0 | 0.00 --- | 0.16 0.06 | 0.0000 --- | 0.0000 --- | 85.00 13.23 |
| 250 | 5 | 0 | 7.0 | 0.71 0.17 | 0.16 0.06 | 0.0023 0.0010 | 0.0222 0.0083 | 35.00 13.23 |
| 300 | 2 | 0 | 2.0 | 1.00 --- | 0.04 0.03 | 0.0009 0.0006 | 0.0400 0.0000 | --- --- |
| <u>I) Perennators (B^{***},C⁺,G⁺,H^{**})</u> | | | | | | | | |
| 0 | 2 | 0 | 20.0 | 0.01 0.07 | 1.00 0.00 | 0.0020 0.0013 | 0.0021 0.0015 | 75.00 6.99 |
| 50 | 16 | 0 | 18.0 | 0.89 0.07 | 0.90 0.07 | 0.0160 0.0018 | 0.0320 0.0048 | 28.13 6.63 |
| 100 | 0 | 0 | 2.0 | 0.00 --- | 0.10 0.07 | 0.0000 --- | 0.0000 --- | --- --- |
| 150 | 0 | 0 | 2.0 | 0.00 --- | 0.10 0.07 | 0.0000 --- | 0.0000 --- | --- --- |
| 200 | 0 | 0 | 2.0 | 0.00 --- | 0.10 0.07 | 0.0000 --- | 0.0000 --- | --- --- |
| 250 | 2 | 0 | 2.0 | 1.00 --- | 0.10 0.07 | 0.0020 0.0013 | 0.0400 0.0000 | --- --- |

Table A1, cont'd

| X | Dx | Wx | Nx | qx (SE) | lx (SE) | PDF (SE) | HAZ (SE) | ex (SE) |
|----------------------------------|-----|----|--------|-----------|-----------|---------------|---------------|-------------|
| <u>Entire population, pooled</u> | | | | | | | | |
| 0 | 302 | 0 | 1399.0 | 0.22 0.01 | 1.00 0.00 | 0.0043 0.0002 | 0.0048 0.0003 | 71.00 0.99 |
| 50 | 946 | 1 | 1096.5 | 0.86 0.01 | 0.78 0.01 | 0.0135 0.0003 | 0.0303 0.0006 | 28.98 0.88 |
| 100 | 105 | 0 | 150.0 | 0.70 0.04 | 0.11 0.01 | 0.0015 0.0001 | 0.0215 0.0018 | 35.71 2.92 |
| 150 | 13 | 0 | 45.0 | 0.29 0.07 | 0.03 0.01 | 0.0002 0.0001 | 0.0068 0.0018 | 121.59 7.62 |
| 200 | 0 | 0 | 32.0 | 0.00 -.- | 0.02 0.00 | 0.0000 -.- | 0.0000 -.- | 86.36 6.43 |
| 250 | 22 | 0 | 32.0 | 0.69 0.08 | 0.02 0.00 | 0.0003 0.0001 | 0.0210 0.0038 | 36.36 6.43 |
| 300 | 4 | 0 | 10.0 | 0.40 0.15 | 0.01 0.00 | 0.0001 0.0000 | 0.0100 0.0048 | -.- -.- |
| 350 | 6 | 0 | 6.0 | 1.00 -.- | 0.00 0.00 | 0.0001 0.0000 | 0.0400 0.0000 | -.- -.- |

Notes: X = days from marking; Dx = Number dying in interval beginning day x;

Wx = no. lost in interval; Nx = effective size in interval;

qx = single interval mortality prob.; lx = cumulative survivorship;

PDF = survival probability density function, $-d/dt(lx)$;

HAZ = hazard function or force of mortality, $d/dt (\ln(lx))$;

ex = median life expectancy; SE = standard error of estimate.

Tests for equality among strata: logrank: $\chi^2=422.58$, $df=8$, $p<0.0001$;

Wilcoxon: $\chi^2=403.58$, $df=8$, $p<0.0001$.

Letters in parentheses give strata shown to differ by pairwise Kruskal-Wallis tests.

Symbols give significance levels: + .10> p >.05; * p <.05; ** p <.01; *** p <.001.

Table A2. Life table estimates and standard errors, Portal 1986.

| X | Dx | Wx | Nx | qx (SE) | lx (SE) | PDF (SE) | HAZ (SE) | ex (SE) |
|---|-----|----|-------|-----------|-----------|---------------|---------------|-------------|
| <u>A) 1 cm Non-Spring-Flowerers (B^{***},C^{***},D^{***},E^{***})</u> | | | | | | | | |
| 0 | 170 | 0 | 508.0 | 0.33 0.02 | 1.00 0.00 | 0.0067 0.0004 | 0.0080 0.0006 | 65.86 2.138 |
| 50 | 264 | 2 | 337.0 | 0.78 0.02 | 0.67 0.02 | 0.0104 0.0004 | 0.0258 0.0012 | 31.91 1.74 |
| 100 | 22 | 0 | 72.0 | 0.31 0.05 | 0.14 0.02 | 0.0009 0.0002 | 0.0072 0.0015 | 66.28 4.93 |
| 150 | 43 | 0 | 50.0 | 0.86 0.04 | 0.10 0.01 | 0.0017 0.0003 | 0.0302 0.0030 | 29.07 4.11 |
| 200 | 7 | 0 | 70.0 | 1.00 --- | 0.01 0.01 | 0.0003 0.0001 | 0.0400 0.0000 | --- --- |
| <u>B) 2 cm Non-Spring-Flowerers(A^{***},C^{**},D^{**},E^{***})</u> | | | | | | | | |
| 0 | 143 | 0 | 548.0 | 0.26 0.02 | 1.00 0.00 | 0.0052 0.0004 | 0.0060 0.0005 | 74.97 2.23 |
| 50 | 262 | 1 | 404.5 | 0.64 0.02 | 0.74 0.02 | 0.0096 0.0004 | 0.0192 0.0010 | 38.60 1.92 |
| 100 | 46 | 0 | 142.0 | 0.32 0.04 | 0.26 0.02 | 0.0017 0.0002 | 0.0077 0.0011 | 63.74 3.27 |
| 150 | 91 | 0 | 96.0 | 0.94 0.02 | 0.18 0.02 | 0.0033 0.0003 | 0.0360 0.0016 | 26.37 2.69 |
| 200 | 5 | 0 | 5 | 1.00 --- | 0.01 0.00 | 0.0002 0.0001 | 0.0400 0.0000 | --- --- |

Table A2, cont'd

| X | Dx | Wx | Nx | qx (SE) | lx (SE) | PDF (SE) | HAZ (SE) | ex (SE) |
|--|-----|----|-------|-----------|-----------|---------------|---------------|-------------|
| C) 3 cm Non-Spring-Flowerers (A ^{***} , B ^{**} , E ^{***}) | | | | | | | | |
| 0 | 39 | 0 | 229.0 | 0.17 0.02 | 1.00 0.00 | 0.0034 0.0005 | 0.0037 0.0006 | 86.46 3.65 |
| 50 | 103 | 2 | 189.0 | 0.55 0.04 | 0.83 0.02 | 0.0090 0.0007 | 0.0150 0.0014 | 45.87 3.34 |
| 100 | 21 | 0 | 85.0 | 0.24 0.04 | 0.38 0.03 | 0.0019 0.0004 | 0.0056 0.0012 | --- --- |
| 150 | 64 | 0 | 64.0 | 1.00 --- | 0.28 0.03 | 0.0057 0.0006 | 0.0400 0.0000 | --- --- |
| D) 4+ cm Non-Spring-Flowerers (A ^{***} , B ^{**} , E ^{***}) | | | | | | | | |
| 0 | 10 | 0 | 79.0 | 0.13 0.04 | 1.00 0.00 | 0.0025 0.0008 | 0.0027 0.0009 | 93.38 6.54 |
| 50 | 34 | 0 | 69.0 | 0.49 0.06 | 0.87 0.04 | 0.0086 0.0011 | 0.0131 0.0021 | 51.56 12.98 |
| 100 | 16 | 0 | 35.0 | 0.46 0.08 | 0.44 0.06 | 0.0041 0.0009 | 0.0119 0.0028 | --- --- |
| 150 | 19 | 0 | 19.0 | 1.00 --- | 0.24 0.04 | 0.0048 0.0010 | 0.0400 0.0000 | --- --- |

Table A2, cont'd

| X | Dx | Wx | Nx | qx (SE) | lx (SE) | PDF (SE) | HAZ (SE) | ex (SE) | | | | | |
|--|-----|----|--------|---------|---------|----------|----------|---------|--------|--------|--------|--------|------|
| <u>E) Spring Flowerers (A***,B***,C***,D***)</u> | | | | | | | | | | | | | |
| 0 | 2 | 0 | 39.0 | 0.05 | 0.04 | 1.00 | 0.00 | 0.0010 | 0.0007 | 0.0011 | 0.0007 | 153.75 | 7.81 |
| 50 | 8 | 0 | 37.0 | 0.22 | 0.07 | 0.94 | 0.04 | 0.0041 | 0.0013 | 0.0048 | 0.0017 | 106.25 | 7.60 |
| 100 | 8 | 0 | 29.0 | 0.28 | 0.08 | 0.74 | 0.07 | 0.0041 | 0.0013 | 0.0064 | 0.0022 | 66.25 | 6.73 |
| 150 | 20 | 0 | 21.0 | 0.95 | 0.04 | 0.54 | 0.08 | 0.0103 | 0.0016 | 0.0364 | 0.0034 | 26.25 | 5.73 |
| 200 | 1 | 0 | 1.0 | 1.00 | --- | 0.03 | 0.03 | 0.0005 | 0.0005 | 0.0400 | 0.0000 | --- | --- |
| <u>Entire population, pooled</u> | | | | | | | | | | | | | |
| 0 | 364 | 0 | 1403.0 | 0.26 | 0.01 | 1.00 | 0.00 | 0.0052 | 0.0002 | 0.0060 | 0.0003 | 75.09 | 1.39 |
| 50 | 671 | 5 | 1036.5 | 0.64 | 0.01 | 0.74 | 0.01 | 0.0096 | 0.0003 | 0.0191 | 0.0007 | 38.62 | 1.20 |
| 100 | 113 | 0 | 363.0 | 0.31 | 0.02 | 0.26 | 0.01 | 0.0016 | 0.0002 | 0.0074 | 0.0007 | 64.45 | 2.01 |
| 150 | 237 | 0 | 250.0 | 0.94 | 0.01 | 0.18 | 0.01 | 0.0034 | 0.0002 | 0.0360 | 0.0010 | 26.37 | 1.67 |
| 200 | 13 | 0 | 13.0 | 1.00 | --- | 0.01 | 0.00 | 0.0002 | 0.0001 | 0.0400 | 0.0000 | --- | --- |

Notes: Notation as in table A1.

Tests for equality among strata: logrank, $\chi^2=79.64$, $df=4$, $p<0.0001$

Wilcoxon, $\chi^2=95.79$, $df=4$, $p<0.0001$

Table A3. Life table estimates and standard errors, Organ Pipe 1985.

| X | Dx | Nx | qx | (SE) | lx | (SE) | PDF | (SE) | HAZ | (SE) |
|-----------------------------|-----|-------|------|------|------|------|--------|--------|--------|--------|
| <u>Spring-Flowerers</u> | | | | | | | | | | |
| 0 | 8 | 37.0 | 0.22 | 0.07 | 1.00 | 0.00 | 0.0037 | 0.0088 | 0.0041 | 0.0014 |
| 59 | 10 | 91.5 | 0.11 | 0.03 | 0.78 | 0.06 | 0.0050 | 0.0065 | 0.0068 | 0.0021 |
| 76 | 38 | 119.5 | 0.32 | 0.04 | 0.69 | 0.06 | 0.0171 | 0.0101 | 0.0291 | 0.0046 |
| 89 | 98 | 137.5 | 0.71 | 0.04 | 0.47 | 0.05 | 0.0141 | 0.0087 | 0.0461 | 0.0039 |
| 113 | 32 | 94.0 | 0.34 | 0.04 | 0.13 | 0.02 | 0.0036 | 0.0029 | 0.0316 | 0.0055 |
| 126 | 7 | 65.0 | 0.11 | 0.04 | 0.09 | 0.01 | 0.0004 | 0.0008 | 0.0042 | 0.0016 |
| 153 | 19 | 55.0 | 0.34 | 0.06 | 0.08 | 0.01 | 0.0006 | 0.0011 | 0.0087 | 0.0020 |
| 201 | -- | 33.0 | --- | --- | 0.05 | 0.01 | --- | --- | --- | --- |
| <u>Non-Spring-Flowerers</u> | | | | | | | | | | |
| 0 | 72 | 113.0 | 0.64 | 0.04 | 1.00 | 0.00 | 0.0108 | 0.0059 | 0.0158 | 0.0017 |
| 59 | 92 | 216.0 | 0.43 | 0.03 | 0.36 | 0.04 | 0.0091 | 0.0055 | 0.0318 | 0.0032 |
| 76 | 74 | 192.5 | 0.38 | 0.04 | 0.20 | 0.02 | 0.0062 | 0.0037 | 0.0366 | 0.0041 |
| 89 | 180 | 205.5 | 0.88 | 0.02 | 0.12 | 0.01 | 0.0047 | 0.0035 | 0.0649 | 0.0030 |
| 113 | 40 | 118.0 | 0.34 | 0.04 | 0.01 | 0.00 | 0.0004 | 0.0004 | 0.0314 | 0.0049 |
| 126 | 19 | 85.0 | 0.22 | 0.04 | 0.01 | 0.00 | 0.0001 | 0.0001 | 0.0093 | 0.0021 |
| 153 | 18 | 62.5 | 0.29 | 0.06 | 0.00 | 0.00 | 0.0000 | 0.0001 | 0.0070 | 0.0016 |
| 201 | -- | 43.0 | --- | --- | 0.00 | 0.00 | --- | --- | --- | --- |

Table A3, cont'd

| X | Dx | Nx | qx (SE) | lx (SE) | PDF (SE) | HAZ (SE) |
|----------------------------------|-----|-------|-----------|-----------|---------------|---------------|
| <u>Entire population, pooled</u> | | | | | | |
| 0 | 80 | 150.0 | 0.53 0.04 | 1.00 0.00 | 0.0090 0.0053 | 0.0123 0.0013 |
| 59 | 102 | 307.5 | 0.33 0.03 | 0.46 0.04 | 0.0091 0.0045 | 0.0234 0.0023 |
| 76 | 112 | 312.0 | 0.36 0.03 | 0.31 0.03 | 0.0086 0.0038 | 0.0337 0.0031 |
| 89 | 278 | 343.0 | 0.81 0.02 | 0.19 0.02 | 0.0068 0.0036 | 0.0568 0.0025 |
| 113 | 72 | 212.0 | 0.34 0.03 | 0.03 0.00 | 0.0010 0.0006 | 0.0315 0.0036 |
| 126 | 26 | 150.0 | 0.17 0.03 | 0.02 0.00 | 0.0053 0.0002 | 0.0070 0.0014 |
| 153 | 37 | 117.5 | 0.31 0.04 | 0.02 0.00 | 0.0045 0.0002 | 0.0127 0.0020 |
| 201 | -- | 76.0 | --- --- | 0.01 0.00 | --- --- | --- --- |

Notes: Notation as in table A1.

Nx not monotonically decreasing due to addition of plants to study; see Methods.

Tests for homogeneity among strata: Logrank, $\chi^2=29.88$, $df=1$, $p<0.0001$

Wilcoxon, $\chi^2=42.16$, $df=1$, $p<0.0001$

Table A4. Life table estimates and standard errors, Portal 1985.

| X | Dx | Wx | Nx | qx | (SE) | lx | (SE) | PDF | (SE) | HAZ | (SE) |
|---|-----------|-----------|-----------|-----------|-------------|-----------|-------------|------------|-------------|------------|-------------|
| <u>A) 1 cm Non-Spring-Flowerers (B^{***},C^{***},D^{***})</u> | | | | | | | | | | | |
| 0 | 18 | 0 | 68.00 | 0.26 | 0.05 | 1.00 | 0.00 | 0.0132 | 0.0120 | 0.0153 | 0.0036 |
| 20 | 24 | 0 | 50.00 | 0.48 | 0.07 | 0.74 | 0.05 | 0.0176 | 0.0130 | 0.0316 | 0.0061 |
| 40 | 5 | 0 | 26.00 | 0.19 | 0.08 | 0.38 | 0.05 | 0.0037 | 0.0070 | 0.0106 | 0.0047 |
| 60 | 2 | 0 | 21.00 | 0.10 | 0.06 | 0.31 | 0.03 | 0.0015 | 0.0045 | 0.0050 | 0.0035 |
| 80 | 0 | 0 | 18.00 | 0.00 | 0.00 | 0.28 | 0.02 | 0.0000 | 0.0000 | 0.0000 | 0.0000 |
| 100 | 1 | 2 | 17.00 | 0.06 | 0.06 | 0.28 | 0.00 | 0.0008 | 0.0036 | 0.0030 | 0.0030 |
| 120 | 0 | 0 | 16.00 | 0.00 | 0.00 | 0.26 | 0.02 | 0.0000 | 0.0000 | 0.0000 | 0.0000 |
| <u>B) 2 cm Non-Spring-Flowerers(A^{***},D^{***})</u> | | | | | | | | | | | |
| 0 | 10 | 0 | 96.50 | 0.10 | 0.03 | 1.00 | 0.00 | 0.0052 | 0.0069 | 0.0055 | 0.0017 |
| 20 | 11 | 1 | 86.00 | 0.13 | 0.04 | 0.90 | 0.03 | 0.0057 | 0.0073 | 0.0068 | 0.0021 |
| 40 | 8 | 0 | 75.00 | 0.11 | 0.04 | 0.78 | 0.03 | 0.0042 | 0.0063 | 0.0056 | 0.0020 |
| 60 | 5 | 0 | 66.50 | 0.08 | 0.03 | 0.70 | 0.03 | 0.0026 | 0.0051 | 0.0039 | 0.0017 |
| 80 | 0 | 1 | 58.50 | 0.00 | 0.00 | 0.65 | 0.02 | 0.0000 | 0.0000 | 0.0000 | 0.0000 |
| 100 | 8 | 5 | 56.00 | 0.14 | 0.05 | 0.65 | 0.00 | 0.0046 | 0.0068 | 0.0077 | 0.0027 |
| 120 | 0 | 0 | 48.00 | 0.00 | 0.00 | 0.55 | 0.03 | 0.0000 | 0.0000 | 0.0000 | 0.0000 |

Table A4, cont'd

| X | Dx | Wx | Nx | qx (SE) | lx (SE) | PDF (SE) | HAZ (SE) |
|---|-----------|-----------|-----------|----------------|----------------|-----------------|-----------------|
| <u>C) 3 + cm Non-Spring-Flowerers (A^{***},D[*])</u> | | | | | | | |
| 0 | 5 | 0 | 100.50 | 0.05 0.02 | 1.00 0.00 | 0.0025 0.0048 | 0.0026 0.0011 |
| 20 | 9 | 1 | 95.00 | 0.09 0.03 | 0.95 0.02 | 0.0045 0.0064 | 0.0050 0.0017 |
| 40 | 9 | 0 | 85.50 | 0.11 0.03 | 0.86 0.03 | 0.0045 0.0064 | 0.0056 0.0018 |
| 60 | 6 | 1 | 76.00 | 0.08 0.03 | 0.77 0.03 | 0.0030 0.0053 | 0.0041 0.0017 |
| 80 | 0 | 0 | 69.00 | 0.00 0.00 | 0.71 0.02 | 0.0000 0.0000 | 0.0000 0.0000 |
| 100 | 8 | 2 | 68.00 | 0.12 0.04 | 0.71 0.00 | 0.0042 0.0062 | 0.0063 0.0022 |
| 120 | 0 | 0 | 60.00 | 0.00 0.00 | 0.63 0.03 | 0.0000 0.0000 | 0.0000 0.0000 |

Table A4, cont'd

| X | Dx | Wx | Nx | qx | (SE) | lx | (SE) | PDF | (SE) | HAZ | (SE) |
|------------------------------------|-----------|-----------|-----------|-----------|-------------|-----------|-------------|------------|-------------|------------|-------------|
| <u>Non-Spring-Flowerers pooled</u> | | | | | | | | | | | |
| 0 | 60 | 0 | 489.00 | 0.12 | 0.01 | 1.00 | 0.00 | 0.0061 | 0.0033 | 0.0065 | 0.0008 |
| 20 | 83 | 6 | 425.50 | 0.20 | 0.02 | 0.88 | 0.01 | 0.0086 | 0.0038 | 0.0108 | 0.0012 |
| 40 | 44 | 1 | 340.00 | 0.13 | 0.02 | 0.71 | 0.02 | 0.0046 | 0.0029 | 0.0069 | 0.0010 |
| 60 | 28 | 4 | 293.50 | 0.10 | 0.02 | 0.61 | 0.01 | 0.0029 | 0.0024 | 0.0050 | 0.0009 |
| 80 | 0 | 1 | 255.00 | 0.00 | 0.00 | 0.56 | 0.01 | 0.0000 | 0.0000 | 0.0000 | 0.0000 |
| 100 | 27 | 20 | 245.00 | 0.11 | 0.02 | 0.56 | 0.00 | 0.0031 | 0.0025 | 0.0058 | 0.0011 |
| 120 | 0 | 0 | 218.00 | 0.00 | 0.00 | 0.49 | 0.01 | 0.0000 | 0.0000 | 0.0000 | 0.0000 |

Table A4, cont'd

| X | Dx | Wx | Nx | qx (SE) | lx (SE) | PDF (SE) | HAZ (SE) | | | | |
|--|----|----|--------|---------|---------|----------|----------|--------|--------|--------|--------|
| <u>D) Spring Flowerers (A^{***},B^{***},C[*])</u> | | | | | | | | | | | |
| 0 | 1 | 0 | 71.50 | 0.01 | 0.01 | 1.00 | 0.00 | 0.0007 | 0.0031 | 0.0007 | 0.0007 |
| 20 | 2 | 1 | 70.00 | 0.03 | 0.02 | 0.99 | 0.01 | 0.0014 | 0.0044 | 0.0014 | 0.0010 |
| 40 | 0 | 0 | 68.00 | 0.00 | 0.00 | 0.96 | 0.02 | 0.0000 | 0.0000 | 0.0000 | 0.0000 |
| 60 | 4 | 0 | 68.00 | 0.06 | 0.03 | 0.96 | 0.00 | 0.0028 | 0.0061 | 0.0030 | 0.0015 |
| 80 | 0 | 0 | 61.00 | 0.00 | 0.00 | 0.90 | 0.03 | 0.0000 | 0.0000 | 0.0000 | 0.0000 |
| 100 | 5 | 6 | 58.00 | 0.09 | 0.04 | 0.90 | 0.00 | 0.0039 | 0.0074 | 0.0045 | 0.0020 |
| 120 | 0 | 0 | 53.00 | 0.00 | 0.00 | 0.82 | 0.03 | 0.0000 | 0.0000 | 0.0000 | 0.0000 |
| <u>All Categories pooled</u> | | | | | | | | | | | |
| 0 | 61 | 0 | 507.00 | 0.12 | 0.01 | 1.00 | 0.00 | 0.0060 | 0.0032 | 0.0064 | 0.0008 |
| 20 | 84 | 6 | 442.50 | 0.19 | 0.02 | 0.88 | 0.01 | 0.0083 | 0.0037 | 0.0105 | 0.0011 |
| 40 | 44 | 1 | 356.00 | 0.12 | 0.02 | 0.71 | 0.02 | 0.0044 | 0.0028 | 0.0066 | 0.0010 |
| 60 | 29 | 4 | 309.50 | 0.09 | 0.02 | 0.62 | 0.01 | 0.0029 | 0.0023 | 0.0049 | 0.0009 |
| 80 | 0 | 1 | 270.00 | 0.00 | 0.00 | 0.57 | 0.01 | 0.0000 | 0.0000 | 0.0000 | 0.0000 |
| 100 | 28 | 20 | 260.00 | 0.11 | 0.02 | 0.57 | 0.00 | 0.0030 | 0.0024 | 0.0057 | 0.0011 |
| 120 | 0 | 0 | 232.00 | 0.00 | 0.00 | 0.51 | 0.01 | 0.0000 | 0.0000 | 0.0000 | 0.0000 |

Notes: Notation as in table A1.

Tests for homogeneity among strata: logrank, $\chi^2=72.64$, $df=3$, $p<0.0001$

Wilcoxon, $\chi^2=79.67$, $df=3$, $p<0.0001$

Tests for homogeneity between spring flowerers and pooled non-spring-flowerers:

logrank, $\chi^2=25.59$, $df=1$, $p<0.0001$

Wilcoxon, $\chi^2=27.33$, $df=1$, $p<0.0001$

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